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THE CYTOGENY OF PODARKE OBSCURA (VERRILL)

A DISSERTATION
Submitted to the Faculties of the Graduate Schools of Arts,
Literature, and Science, in candidacy for the degree of
DOCTOR OF PHILOSOPHY
(Department of Zoölogy)
March 2, 1899

BY

AARON LOUIS TREADWELL

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AARON L. TREADWELL.

CONTENTS.

PART I.—DESCRIPTIVE.

PAGE
Introductory 399
Egg-Laying and Methods 400
One to Two Cells 404
Two to Four Cells 404
Four to Eight Cells 406
Eight to Sixteen Cells 407
Sixteen to Thirty-two Cells 407
Thirty-two to Sixty-four Cells 408
First Group of Ectomeres 412
Second Group of Ectomeres 419
Third Group of Ectomeres 425
Larval Mesoblast 427
Fourth Group of Ectomeres 429
Fifth Group of Ectomeres 433
Trochophore 434

PART II. — GENERAL CONSIDERATIONS.

Axial Relations 438
Types of Cleavage 438
Cell Mechanics 440
Equal and Unequal Cleavage 441
Mesoblast and Larval Mesoblast 449
Cell and Regional Homology 455

THE following investigation, begun in 1891, has been carried on at the Marine Biological Laboratory at Woods Holl, Mass., in the Zoölogical Laboratory of the University of Chicago, and in the intervals of teaching at Miami University. For many helpful suggestions I am indebted to my friends, Drs. C. M. Child, E. G. Conklin, and A. D. Mead. I desire especially to acknowledge my indebtedness to Professor C. O. Whitman, without whose friendly encouragement the work would hardly have been completed. In the preparation of my drawings I am indebted to my wife, who has finished from my camera sketches all of the figures which illustrate this paper.

Podarke obscura is a small Hesionid, abundant in various localities at Woods Holl, Mass. The species was described and named by Verrill (No. 30), who says that at night during July and August they come to the surface and swim about "in vast numbers." I have never been able to confirm the latter observation and have found only a few when towing at night, these seeming rather to be attached to bits of floating eelgrass than swimming free. In the "Eel Pond" and in "Little Harbor" they are abundant, lying in the soft, flocculent surface mud and clinging to the eelgrass a short distance from the bottom. It is almost hopeless to attempt to pick the animals from the mud, and I have found the best way to collect is to sweep through the grass with a strong net. (I used for this purpose a wooden-rimmed flour sieve.) The animals remain in the sieve and can easily be jarred into a bucket, while the finer dirt passes through with the water. They were then transferred to clean water in glass dishes in the laboratory, where with only an occasional change of water they will live indefinitely. Both in their natural environment and in captivity they seem rather sluggish, though if irritated they will swim rapidly away from the disturbing object. They will burrow quickly into any dirt or sediment that may be in the dish, but seem in no way inconvenienced if forced to live in clean water. The occurrence of bifid monsters is very common, a number of such cases having been described by Andrews (No. 1).

Specimens in captivity lay their eggs from 7.30 to 9 P.M., usually on the second or third, rarely on the first, night after they are brought into the laboratory. The eggs have no albuminous coat, and hence when extruded sink rapidly to the bottom of the dish, where, if the water be clean, they may easily be recognized and picked out with a pipette. A simpler expedient is to strain the water through a fine cloth, through whose meshes the eggs will pass, leaving the adult annelids behind.

Artificial fertilization, though tried repeatedly and at various times of the day, was never successful, unless the eggs had been laid in the normal manner by the female. Then it was perfectly possible to cut sperm from the body of the male and fertilize. Since, as already stated, the normal time of laying is from 7.30 to 9 P.M., many important early stages are passed through before daylight (the embryo begins to swim at the completion of the 64-cell stage, or about the fifth hour of development), and since the small size and opacity of the embryo make it an unfavorable object for study by artificial light, an attempt was made to delay the process of laying. Although a number of devices which had proved successful in other forms were tried, they were wholly without success. If the females are put on ice, or in a very cool place, overnight, they will hold their eggs until about daylight the next morning, but such eggs almost invariably developed abnormally; and the same result followed if for any reason the eggs were laid at other than the regular time. In one case only did I find eggs which must have been laid about 4 A.M. developing normally. It is not at all improbable that modifications of the cooling method might have proved successful, but for the purposes of this paper preserved material was so much more satisfactory than fresh that I have relied almost entirely on that, merely using the fresh, where possible, for corroboration. Cilia can of course be seen better in living than in preserved material, but the history of cells can best be made out on stained specimens where the karyokinetic figures give absolutely accurate evidence of cell origin.

When the sexual products are ripe, the sexes may be easily distinguished by the characteristic color of the ova and sperm seen through the semi-transparent body wall; the females being a seal brown, the males a cream color. I found that the most convenient way was to isolate the sexes, which seems in no way to affect the time of egg-laying, and when laid to transfer the eggs to fresh water and fertilize with sperm cut from the body of the male. In this way the precise time of fertilization can be controlled, something which cannot always be done if the sexes are together; and the difficulties arising from an excessive number of sperm collected on the surface of the egg can be avoided.

While emitting the sexual products, the female usually crawls slowly along the bottom of the dish, the eggs streaming out from both sides of the body through openings at the base of the parapodia. Occasionally one will be found swimming with considerable rapidity during this process. The males are usually much more active at this time, though there is never anything like the amount of activity displayed by some other free-swimming annelids, *e.g.*, Nereis.

Material obtained and fertilized in this way was preserved at intervals of fifteen minutes for the first twelve hours, and at rather longer intervals for the later stages. There is so much variation in rate of development in the different lots, due apparently to temperature conditions, that time records are of little value, and I have not attempted to keep them after the first few divisions.

For preserving, I have found Kleinenberg's picro sulphuric (dilute) and picro acetic (made with 1% acetic) the most useful, the latter especially, when followed by Delafield's haematoxylin[1] (acidified), giving beautiful results with surface views. Flemming's fluid, though practically worthless for surface views, preserves cilia well, and gives better preservation for sectioning than the picro acetic. The specimens, preserved and stained as above, were cleared in clove oil and mounted in the same medium underneath a long cover-glass, supported at one end by a bit of capillary glass tubing. This method, for which I am indebted to my friend Dr. C. M. Child, has proved much more satisfactory than to mount in balsam, as the specimens can be rolled into any desired position and drawn with a camera as soon as they are mounted.

In the main I have followed Mead's nomenclature (No. 22) with certain modifications suggested in conference with Dr. Child, whose work on Arenicola has been carried on at the same time as this. The successive generations of "macromeres" we propose to designate by capital letters, with the generation indicated by a coefficient, while the "micromeres" are indicated by small letters, each with a coefficient indicating the generation and a subscript indicating its position in the generation. Thus, A, B, C, D form the 4-cell stage. At their next division from A arises 1A and 1a; from B, 1B and 1b, etc. 1A then divides into 2A and 2a, while 1a divides into $1a_1$ and $1a_2$.

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[1] I am under great obligations to Dr. Conklin for suggestions as to the use of this method.

We have continued the use of the terms "dexiotropic" and "leiotropic" to indicate the direction of the spiral cleavages, but propose the terms "dextral" and "sinistral" to designate the respective daughter-cells resulting from a spiral cleavage, reserving the terms "right" and "left" to apply to the sides of the bilaterally symmetrical body. Thus, in a dexiotropic cleavage, the upper cell when viewed from the animal pole would lie to the right, and is the "dextral" cell, the other is "sinistral," and *vice versa* in a leiotropic cleavage. In all cases the cell nearer the vegetative pole has the larger exponent, regardless of absolute size. When a cleavage is meridional, the sinistral cell receives the smaller exponent.

This method has one disadvantage, in that symmetrically placed cells which arose by a meridional division do not receive corresponding subscripts. Thus (see Pl. XXXVIII, Fig. 27), $3c_2$ and $3d_2$ divide in a meridional direction and so that their products are symmetrically placed with respect to the median plane of the embryo. After one more division their larger daughter-cells become the larval mesoblast. One of these cells is $3c_{2.1}$, and the other $3d_{2.2}$, according to the proposed system. I believe, however, the advantages of the system will outweigh any disadvantages resulting from a possible confusion. This nomenclature differs from that adopted in my preliminary paper (No. 29, *a*), but seems enough of an improvement over that to warrant the change.

Cleavage.

The eggs are small, measuring 62.9 μ in diameter, and are, in the fresh condition, very opaque. As already stated, they are not provided with any albuminous coating, and when laid sink rapidly to the bottom of the dish. They are usually more or less irregular when first laid, but rapidly become spherical or nearly so. In some cases there has seemed to be a certain amount of axial differentiation, but these differences are not constant. A thin membrane surrounds the egg, and remains attached to it until the latest stage I have studied. Whether, as is commonly stated to be the case among annelids, it becomes the cuticle of the adult, I cannot say. It is smooth in the living egg, but becomes more or less wrinkled under the influence of reagents. Except in Fig. 1, I have not attempted to represent it in the plates.

Soon after laying, the first polar spindle appears, and the eggs remain in this condition until fertilized. A study of the maturation and fertilization stages is reserved for a future paper, and the present account begins with the first cleavage.

The first cleavage begins, with very slight variations in time, one hour after fertilization. At this time the animal pole is indicated by the position of the polar globules and by a certain amount of protoplasmic differentiation easily seen in stained material. The vegetal pole of the egg stains very slightly with haematoxylin, and has a granular appearance, while the animal half is much more homogeneous in texture and stains more deeply. The first spindle lies slightly nearer the animal than the vegetal pole. (See Pl. XXXVI, Fig. 1.)

The first cleavage furrow cuts rapidly through the egg, sinking down more rapidly at the upper than at the lower pole (*cf.* Wilson, No. 34, *d*, and Mead, No. 22), and the 2-cell stage results. (See Pl. XXXVI, Fig. 2.) Here it will be seen that the first cleavage is exactly equal. The two nuclei are directly opposite one another, there being no indication of the rotation described by Conklin in the 2-celled stage of Crepidula. A lenticular cleavage cavity is formed, which persists and becomes the large cleavage cavity of the later stages. (See Text-Figs. 1 and 2.)

Two to Four Cells. — The next three cleavages follow one another at intervals of approximately fifteen minutes, but beyond this, time records are of little value. The eggs of the same lot are usually in practically the same stage at any one time, but owing doubtless to temperature conditions, different lots vary considerably in rapidity of development. (See Mead, No. 22, p. 269.) The 4-cell stage arises from the 2, by the equal division of both cells, there being no large D, as in other annelids. (See Pl. XXXVI, Fig. 3.) The spindles are not quite parallel with one another, so that two cells rotate upward and two downward. As a result, the familiar "cross furrow" appears. This is found at both poles, that at the upper being at right angles with the lower, and considerably shorter than it. The origin and significance of this furrow have been discussed by Conklin (No. 5, *a*), and I can add nothing to what he has said. It is of considerable *practical* importance in Podarke for purposes of orientation. The direction of this furrow at the lower pole is positively the only means of orientation before the completion of the 56-cell stage. I have taken a good deal of pains to ascertain if it remains constant in direction up to that time. There is no doubt that it does, although soon after the completion of the 64-cell stage this direction may be lost, owing to movements of the entomeres whose position determines the existence of the furrow.

The relation of the two first cleavage planes to the body axes is a point on which most investigators have laid considerable stress. In the cytogeny of annelids and mollusks two apparently distinct relations are found. In Nereis (No. 34, *d*), Crepidula (No. 5, *a*), and Limax (No. 17), for example, the second cleavage furrow is said to coincide with the future median plane, while in Amphitrite (No. 22) and Arenicola (No. 4) the quadrants are anterior, median, right, and left. This apparent discrepancy has been explained by Lillie (No. 21) and Conklin (No. 5, *a*) as arising from the fact that only a small part of the furrow, that between the entomeres, has been considered in determining the orientation. Conklin has shown that in annelids and mollusks there is no exception known to the rule that the second and fourth quartettes lie in the median and transverse planes, while the first and third lie between them. An examination also of Wilson's figures of Nereis will show that the second cleavage furrows, *if traced between the ectomeres*, lie at some distance from the median plane of the embryo.

In orienting the embryo of Podarke, it is impossible to rely on the constancy of direction of the polar furrow after the 64-cell stage. Even before they divide to form the fifth group of micromeres, shiftings in position occur (see Pl. XXXVIII, Fig. 27), and immediately after this division invagination begins. From this time on it is impossible to determine their position with any accuracy. Evidently, then, the arrangement of the ectomeres must be considered here, and that offers no exception to the rule formulated above. The second and fourth generations of micromeres lie in the median and transverse planes, the first and third lie between them. The relation of the entomeres to the ectomeres, as is shown before the latter shift their position, is exactly as in Amphitrite and Arenicola. They lie anterior, posterior, right, and left. Owing to the absence of a large D-cell, however, it is not possible to distinguish between the two ends of the second furrow.

Four to Eight Cells. — The spindles of this division appear about fifteen minutes after the completion of the last, and the cells all divide at approximately the same time. The cells are rarely in *exactly* the same stage at any one instant, and I tried to find some indication of an acceleration of development in one quadrant, such as has been described, *e.g.*, in Unio (No. 21). Such an acceleration, if present, would be of great aid in orientation, but I do not believe that any exists. In later stages, at the lower pole, the C and D quadrants divide a little more rapidly than either A or B, but precisely the opposite occurs at the upper pole (see Pl. XXXVII, Figs. 19 and 23, showing the history of the cross), and in no case was there any constant difference between C and D. Neither was it possible, by any staining reactions, to distinguish between the quadrants.

The result of this division is the formation of the first group of ectomeres, which lie on top of the macromeres, but are exactly equal to them in size, or so nearly equal that their differences lie within the limits of error of observation (Pl. XXXVI, Figs. 4 and 5). The division is dexiotropic, and it is interesting to note that here, as in Nereis (No. 34, *d*, p. 387), the spindles show an inclination from the vertical before any external trace of segmentation is visible.

The upper pole is indicated by the presence of the polar globules, which lie between the cells, almost inside the segmentation cavity (Pl. XXXVI, Fig. 5).

Eight to Sixteen Cells. — The 16-cell stage is reached by the division of each cell of the 8 in a leiotropic direction, the divisions all occurring at about the same time (Pl. XXXVI, Figs. 6 and 7). The division at the lower pole is equal and leads to the formation of the second group of ectomeres. It is of importance to note here that all of the cells of this second group are equal in size, as compared with many other annelids, in which a very large 2d, "the first somatoblast," appears. Inasmuch as the history of this cell 2d in Podarke is similar to that in other annelids, I shall also call it the "first somatoblast." At the upper pole the division is more unequal, the upper cell being the larger. (See Pl. XXXVI, Figs. 6 and 7.) Since the eight cells were all equal, it follows that now the largest cells are at the upper pole, and this relation holds until the cross has been broken up into small cells (Pl. XXXVIII, Fig. 23; Pl. XXXIX, Fig. 37). The smaller cells, $1a_2$, $1b_2$, $1c_2$, $1d_2$, divide twice more and form the primary prototroch of the larva. I shall call them, after Mead, the *primary trochoblasts.* The segmentation cavity present as a lenticular space in the 2-cell stage is continued through the later cleavages, and is present as a good-sized cavity at this time. Its proportions a little later than this are shown in Text-Fig. 2.

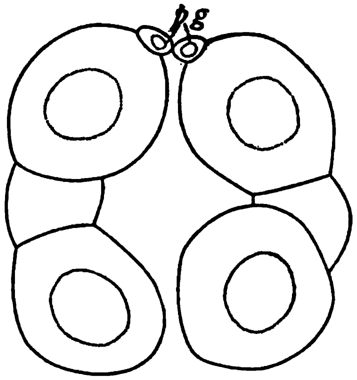

Fig. 1. — Optical section of 16-cell stage, showing large cleavage cavity. *pg*, polar globules.

Sixteen to Thirty-two Cells.—The 32-cell stage is reached by the dexiotropic division of each of the sixteen cells, the transition falling into three well marked subdivisions. *1.* The division of the macromeres to form the third group of ectomeres, which, as we shall see, are not purely ectodermal in destiny, and the division of the upper cells of the embryo giving rise to the "intermediate girdle" cells, which occupy the spaces between the arms of the cross (Pl. XXXVI, Fig. 8). *2.* The division of the primary trochoblasts (Pl. XXXVI, Fig. 9). *3.* The division of the second group of ectomeres (Pl. XXXVI, Fig. 10). At the 32-cell stage, although well-marked size differences have appeared among the cells, the quadrants are still radially symmetrical, and it is impossible, by any differences in size or arrangement of cells, to distinguish them. The polar furrow retains its original direction and enables us to distinguish between the two cleavage planes, but no other orientation mark appears.

At the 32-cell stage the polar globules, which until this time have occupied a position at the upper pole of the egg lying on the inner face of the rounded ectomeres, pass into these latter cells, where they may be seen as small, deeply staining bodies, lying in the protoplasm of the cell (Pl. XXXVI, Fig. 11, *pg*, and Text-Fig. 4). This position they retain for some time. There seems to be no regularity in the process, the bodies sometimes passing into one and sometimes into another of the large cells. Similar observations have been recorded by Mead (No. 22) in Lepidonotus, where, also in the 32-cell stage, the polar globules pass sometimes into one, sometimes into another of the cross cells, or they may even be found in the segmentation cavity; and in Chaetopterus, where the polar globules are ingested by the rosette cells. Grobben (No. 10) finds in Cetochilus that at least one polar globule wanders into the segmentation cavity, where it, presumably, is absorbed. Hatschek (No. 11) in Eupomatus, and Eisig (No. 8) in Capitella, have described a similar fate for the polar globules. (See p. 417.)

Thirty-two to Sixty-four Cells.—The 64-cell stage is "actual" in Podarke, and is reached by the leiotropic division of each of the thirty-two cells. Here, as before, there are three well-marked subdivisions. *1.* Thirty-two to forty cells. The fourth group of micromeres arise at the lower pole (Pl. XXXVII, Fig. 13), and four very small cells, the apical rosette, are divided off from the large cells at the upper pole (Pl. XXXVI, Figs. 11 and 12). It is important to note that the cells of the fourth quartette

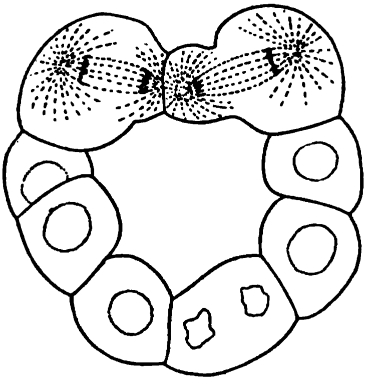

FIG. 2.—Optical section of stage shown in Fig. 11, Pl. XXXVI.

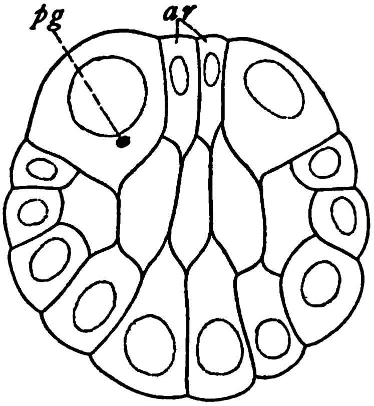

FIG. 3.—Optical section of stage shown in Fig. 15, Pl. XXXVII. *ar*, apical rosette; *pg*, polar globules.

are exactly equal in size; in other words, *there is no large* 4d, and so far as we can tell from observation, the cell containing the mesoderm might be either of two cells lying one at either end of the second cleavage furrow. The spindles at the upper pole are inclined downward a little from the horizontal (Text-Fig. 2). This, combined with the small size of the rosette cells, causes the latter to lie somewhat below the surface (see Pl. XXXVII, Fig. 16, and the Text-Fig. 4). Later, as a result of the pressure of the dividing cross cells, they are forced still farther below the surface. (See Text-Fig. 3.) A similar process has been described by Mead for Lepidonotus (No. 22). As a comparison of Fig. 12 (Pl. XXXVI) with Fig. 27 (Pl. XXXVIII) will show, one result of this division is further to increase the difference in size which has before been noticed between the cells of the upper and those of the lower hemisphere. *2.* Forty to fifty-six cells. (*a*) A division of the trochoblasts to form four cells in each quadrant (Pl. XXXVI, Fig. 12, Pl. XXXVII, Fig. 14, $1d_{2.1}$, $1d_{2.2}$, etc.). These do not divide again, but soon develop cilia and function as the primary prototroch (Pl. XXXVII, Fig. 15, $1d_{2.1.1}$, $1d_{2.1.2}$, $1d_{2.2.1}$, $1d_{2.2.2}$, etc.). This band of ciliated cells is at first broken at four points, but is afterwards completed in a manner to be described later. (*b*) A division of the intermediate girdle cells, $1a_{1.2}$, $1b_{1.2}$, $1c_{1.2}$, $1d_{1.2}$; and (*c*), a division of the third group of micromeres. See Pl. XXXVI, Fig. 12; Pl. XXXVII, Fig. 14, where the spindles of all these divisions are shown. *3.* The second division of the second group of ectomeres (Pl. XXXVII, Fig. 24). This is a most important division, for by it arises the first indication of a difference between the quadrants. It marks, in other words, the first appearance of bilateral symmetry. In three of the quadrants the mode of division is that shown in Pl. XXXVIII, Fig. 25 ($2b_{1.1}$, $2b_{1.2}$, $2b_{2.1}$, $2b_{2.2}$, etc.). In the fourth quadrant the case is different. The dextral cell, $2d_1$, has divided, as in the other quadrants, with a smaller cell above. The sinistral cell, on the other hand, has divided in precisely the opposite way. The larger cell is above, and the smaller cell, which is very much smaller than any products of the division in the other quadrants, is below. This cell lies a little to the right of the second cleavage plane, and nearly over one of the fourth group of micromeres. It can easily be distinguished by its small size and deeply staining nucleus (Pl. XXXVIII, Fig. 26). Later study shows that the "4" micromere, near which it lies, contains the mesoderm. Orientation is now complete, and the quadrant in which the cell in question occurs is the "D" quadrant. A similar cell, occupying a similar position, has been described by Mead (No. 22), Lillie (No. 21), and Conklin (No. 5, *a*) in other annelids and mollusks. The polar furrow retains its original direction up to the time when this cell appears, and this enables us to orient the early cleavage stages.

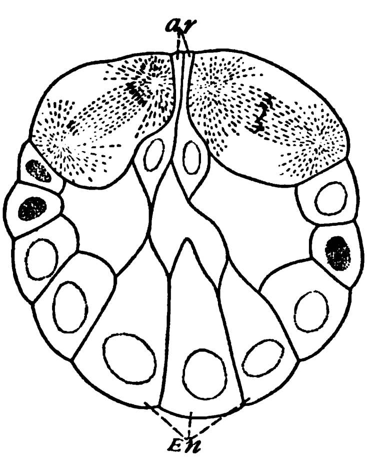

FIG. 4. — Optical section of stage shown in Fig. 16, Pl. XXXVII. In this and later drawings the nuclei of the prototroch cells are stippled.

At about the 40-cell stage strands of protoplasm can be plainly seen reaching across the cleavage cavity, running from the cross and rosette cells to the upper ends of the entomeres (Text-Figs. 3 and 4). From the pointed upper ends of the entomeres in Text-Fig. 5, I believe that the connections exist also in later stages, though I have not been able to make them out on preserved material. Professor E. A. Andrews, who kindly examined some of my preparations at my request, informs me that these processes are undoubtedly protoplasmic, but that he is unable to determine from preserved material whether they are protoplasmic streamings, such as have been described in other animals (see No. 2), or remnants of the primitive continuity which has never been lost. For our present purpose the question is immaterial. Of importance is the fact that protoplasmic connections do exist between blastomeres of relatively late cleavage stages.

The embryo is now composed of sixty-four cells, divided as follows :

1st Quartette	32
2d "	16
3d "	8
4th "	4
Entomeres	4
	64

Three of the quadrants are exactly alike and the fourth differs from them merely in the possession of the small cell, $X_{1.2}$, which lies at what will be the posterior end of the body.

Up to this stage it is evident that Podarke agrees in the character of its segmentation with other annelids and with gasteropods and lamellibranchs. In all cases three quartettes of ectomeres arise in alternating directions. In all cases one member of a fourth quartette is budded off, and this cell is wholly or partially composed of the definitive mesoblast. Usually but not always (*e.g.*, Nereis) the other three members of this fourth quartette appear. Inasmuch as they, together with the remaining macromeres, give rise to the entoderm, the difference is merely that in the one case this division takes place at the surface, in the other, after invagination.

On the other hand, Podarke differs from most other annelids in two important features. The cells of the second and those of the fourth quartettes are all equal in size, whereas in nearly all annelids there is a large 2d and a large 4d. The entomeres also are much larger in other annelids than in Podarke. These differences are important and will be discussed later. (See p. 441.)

Let me repeat that up to the time when the small cell $X_{1.2}$ appears, the polar furrow at the lower pole of the egg retains its original direction. At the 64-cell stage, however, the entomeres elongate inward to a greater or less extent, and the shiftings of position thus caused among the cells may produce a change of direction in the polar furrow. (See Pl. XXXVIII, Fig. 27.) The condition shown in Pl. XXXVIII, Fig. 27, appears only rarely, but often enough to show that the polar furrow can no longer be relied on for orientation.

Since the regular geometrical progression is now lost (some cells, *e.g.*, trochoblasts, do not divide again, while others divide repeatedly), the later history can best be treated by considering each group by itself.

First Group of Ectomeres. — At the 64-cell stage these are arranged as follows:

Trochoblasts	16
Intermediate cells	8
Cross cells	4
Rosette cells	4

The trochoblasts, as already stated, do not divide again, but form the larval locomotor organs. They become elongated as development proceeds, prominent nucleoli appear in their nuclei, and they stain with great difficulty. They are very much narrower than in Amphitrite, agreeing in this respect very closely with Lepidonotus (No. 22). (See Pl. XXXVIII, Figs. 29, 30, etc., *ap′*, etc.) Cilia appear on these cells soon after their last division, about four and a half to five hours after fertilization, and the embryos at first rotate slowly and later swim at the surface, being at first positively heliotropic. The primary prototroch thus formed is at first divided into four distinct areas, the openings between being later filled with cells having a different origin. As long as the separate cells could be distinguished I have designated each by *p'*, with the appropriate letter and number (Pl. XXXVIII, Fig. 25–Pl. XL, Fig. 58). In later stages, where the primary and secondary, and still later, where also the tertiary prototroch cells are not to be distinguished from one another, I have indicated the prototroch merely by *p*, with the appropriate letter to show to which quadrant each portion belongs.

The Intermediate Cells. — The last division of these cells was leiotropic. The next is dexiotropic and leads to the formation of four cells in each quadrant (Pl. XXXVII, Figs. 17 and 18). In three of the quadrants (a, b, and c) the lower product of the division of the dextral cell $1c_{1.2.2.2}$, etc., *completes the primary prototroch* (Pl. XXXIX, Figs. 37 and 38, *ap''*, etc.). They pass into the space between the sets of primary trochoblasts, become ciliated, and function as prototroch cells. I propose to call them the *secondary trochoblasts.* The other products of this division fill the space between the arms of the cross and become a part of the umbrellar ectoderm. For some few divisions I have been able to follow their history, but after the cross cells begin to divide into small cells the two sets intermingle so that it is not possible to distinguish them.

In the fourth quadrant the history of the intermediate cells is very different from that just described. Their first division into four cells is the same, but a little later the lower product of the division of the dextral cell, *i.e.*, the one corresponding to the cell which in other quadrants becomes a part of the prototroch, begins to migrate through the opening in the prototroch, and thus forms a portion of the lower hemisphere. In this migration it is accompanied by part, at least, of its sister-cell, but I think by none of the descendants of the other intermediate cells. These migrating cells push through the break in the prototroch, dividing as they go (Pl. XXXIX, Figs. 42, 44, and 45; Pl. XL, 53, 57, and 58, l_1, l_2, etc., and the cells just dorsal to them). Since the opening persists until late in the development, the process of migration lasts for a considerable time, or until the trochophore is fully formed. In Pl. XL, Figs. 53, 57, and 58, it will be seen that these cells flatten out as they pass downward, one of them, l_1 (Pl. XL, Figs. 53 and 57), elongating very considerably. It immediately adjoins the cell $X_{3.2}$, and the two form a landmark which is unmistakable. Figs. 58 and 59 (Pl. XL) show that the cells which have migrated through the prototroch eventually comprise a large portion of the subumbrella, *fully three-fourths* of it being formed from them. The cell l_1 divides transversely. (See the products of its division, $l_{1.1}$ and $l_{1.2}$, in Pl. XL, Figs. 58 and 59.) Beyond the latter stage I have not followed it. All of these cells become excessively thin and their outlines difficult to follow, so that in the later figures I have indicated only the nuclei. The entoderm cells lie close under the ectoderm, the two being dorsally in actual contact, and it frequently becomes impossible, except in optical section, to determine whether a given nucleus belongs to ectoderm or entoderm. In Pl. XL, Figs. 58 and 59, I have intended to represent only ectoderm nuclei.

A similar migration has been recorded in Amphitrite by Mead (No. 22), but there the number of migrating cells is much less than in Podarke, and they play a much less important part in the formation of the subumbrella.

The Cross. — In the 64-cell stage the cross is composed of four equal cells, radially arranged. At the next division bilateral symmetry appears. It is interesting to note that this is accomplished by a dexiotropic cleavage ; the direction which it ought properly to assume according to the law of alternating cleavages. Fig. 16 (Pl. XXXVII) shows the beginning and Fig. 17 (Pl. XXXVII) the completion of this division. In the latter is seen, also, the beginning of the next divisions of the cross cells in two quadrants. In the latter figure, also, is shown the division of the upper (sinistral) intermediate cell in each quadrant. The result of the first bilateral division of the cross cells is shown in Pl. XXXVII, Fig. 17. Two of the cells have divided unequally, two very nearly equally, so that a vertical plane can be drawn which would cut the embryo into bilaterally symmetrical parts. This plane of symmetry coincides with the plane marked out by the small cell $X_{1.2}$, previously described at the 64-cell stage. The median plane of the embryo is now fully indicated, and orientation is complete. The constant position of the polar furrow up to the 64-cell stage, the appearance of the cell $X_{1.2}$, and the bilaterally symmetrical cross form a series of orientation marks which are unmistakable. We may say, therefore, that in A and B quadrants the first division of the cross is very unequal; in C and D quadrants it is nearly equal.

The Appearance of Bilaterality.

This marking out of a bilateral plane by cleavages which follow a true radial [1] type is important to my mind as indicating that the bilateral divisions have nothing to do with shiftings of material into the median plane, but rather that the bilateral and the radial are distinct in origin. The former having been, so to speak, superimposed upon the latter, the bilaterality of the organism may express itself even in the spiral cleavages.

Bilateral cleavages have not in Podarke such direct reference to the form of the body, as distinct from the head, as Conklin (No. 5, *a*) has described for Crepidula. The first bilateral *cleavage* is at the lower pole (Pl. XXXVIII, Fig. 27), but bilateral divisions appear early and are very prominent at the upper pole as well. Further, as we have seen, bilateral *symmetry* is established before bilateral cleavages appear, and is as marked at the upper as the lower pole.

Of interest in this connection are the following observations: I have seen a few (not more than three were carefully studied) cases where the cross, when formed, is radial and not bilateral. *Each* arm has three equal cells, like the anterior cross arms represented in Pl. XXXVII, Fig. 18. In these same embryos $2d_1$ and $2d_2$ divided just like the other second quartette cells, and no *small* $X_{1.2}$ appeared. In this stage, therefore, the embryo was still radially symmetrical. In one other case three cross arms were alike in having three equal cells, while the fourth was of the posterior cross-arm type. These facts are significant to my mind as indicating a reversion to a radial type of a cleavage which had secondarily become bilateral. The fact that the reversion is always to the radial from the bilateral (from the type of the posterior arm to that of the anterior) and not in the opposite direction is suggestive. The facts are perhaps too few in number to warrant wide inferences, but so far as they go they seem important.

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[1] In this and later discussions I have followed Conklin in classing both "orthoradial" and "spiral" cleavages under the general head of "radial."

The next division of the cross cells emphasizes still more the bilateral symmetry. The division of the basal cells in A and B quadrants, begun in Pl. XXXVII, Fig. 17, is completed in Pl. XXXVII, Fig. 18, and there result three subequal cells in a row in each arm. In C and D quadrants the upper cells divide next, but divide bilaterally, the cells sloping inward (Pl. XXXVII, Fig. 18). In C quadrant the division is equal, in D quadrant unequal. (See Pl. XXXVII, Fig. 19.) This result was so unexpected that I suspected it might be an abnormality, but in examining a large number of preparations I found always the same result.

While this last division is in progress in the basal cells of the posterior arms the terminal cells divide, $1c_{1.1.2.2}$ usually a little in advance of $1d_{1.1.2.2}$. The division is bilateral, and there result two small cells, lying a little farther from the median plane than the center of the large terminal cell. These small cells are very little larger than their nuclei, which stain very deeply, and they lie on top of the cross, between it and the basal cells of the arm. They are excellent landmarks for later study of the embryo, as it is possible at a glance to recognize the C and D quadrants by means of these small deeply staining cells (Pl. XXXVII, Fig. 20).

In Nereis, Wilson (No. 34, *d*) described cells similar to these in origin and position, which he called, provisionally, "head kidneys." In Amphitrite corresponding cells were found by Mead (No. 22), from which arise the huge mucous glands of the trochophore, and Wilson (No. 34, *f*) has since suggested that possibly they are slime glands in Nereis also. In Podarke the next division of the dorsal arms of the cross (Pl. XXXVII, Figs. 20 and 21) buds off one other cell on either side. This cell is very little larger than the first one, and the two pairs remain in this position until very late in the development. The last stage in which I was able to recognize them with certainty was that represented in Pl. XXXVII, Fig. 23. I believe that they become slightly larger in the later stages and form a part of the general ectoderm of the umbrella. Once and only once did I see an indication of a division in one of these cells, $1d_{1.1.2.2.1}$. This I believe was abnormal. They certainly do not become slime glands (excretory glands?) in Podarke, unless the small deeply staining cells scattered over the surface have that function, for there are no such large glands as Mead has described for Amphitrite.

The anterior arms of the cross next divide meridionally. (See the division begun in Pl. XXXVII, Fig. 19, and completed in Pl. XXXVII, Fig. 20.) At their next division a number of small cells appear (Pl. XXXVII, Fig. 22). Note especially the small size of these cells and their deeply staining nuclei. To avoid tedious description I have indicated by junction lines in Pl. XXXVII, Fig. 22, the origin of many of these cells, and have put their divisions in the table, p. 438. In Pl. XXXVII, Figs. 18–23, the outline of the cross is indicated by the heavy line.

Beyond the stage represented in Pl. XXXVII, Fig. 23, I have not attempted to carry the lineage of the anterior (ventral) portion of the umbrella. The cross cells become inextricably confused with the descendants of the intermediate group, and, with possible exceptions, all contribute to the formation of the ventral ectoderm. The exceptions are these. I believe that some of the very small cells are pushed into the cleavage cavity and finally absorbed. Immediately after they are formed they sink below the surface, lying near the bottom of the rather thick ectoderm. A little later dark bodies are seen lying inside the segmentation cavity, and later still they touch the entoderm (see Text-Fig. 8, *ec?*). The point needs reinvestigating before it can be considered absolutely proven, but I believe the fate of the cells is as I have described. A similar process occurs in Crepidula (No. 5, *a*), where, however, the cells are thrown outside the body, and more recently Miss Langenbeck (No. 20) has described, in Microdeutopus, cells which are taken into the segmentation cavity. In Lepidonotus, Mead (No. 22) states that the polar globules pass into the cross cells (see above, p. 417), and he figures them in Figs. 93 and 105. In Podarke, as already stated, the polar globules have a similar fate, but long before the stage corresponding to Mead's Fig. 105 they have completely disappeared. On the other hand, these small cells derived from the ectoderm migrate inward and occupy a position very similar to that of the "polar globules" of the latter figure. This leads to the suggestion that possibly both processes may occur in Lepidonotus also, and that the small cell figured in Fig. 105 is derived from the ectoderm.

In the dorsal arm of the cross, the cells $1c_{1.1.2.1.2}$ and $1d_{1.1.2.1.1}$ next divide (Pl. XXXVII, Fig. 20), and this is followed by the division of $1c_{1.1.2.1.1}$ and $1d_{1.1.2.1.2}$. (See Pl. XXXVII, Figs. 21 and 22, and table, p. 438.) The large terminal cells of the dorsal arms divide considerably later, the divisions being nearly equal. Figs. 22 and 23 (Pl. XXXVII) show the division in C quadrant. (See also Pl. XXXIX, Fig. 42, $1d_{1.1.2.2.2.2}$.) Later than this I have not attempted to follow the cells in detail. They all enter into the formation of the ectoderm on the dorsal side of the umbrella, in which I have been able to make out no specialized organs. Ventrally there are two "eye-spots" and the large "problematic" organs which develop from either the ventral cross cells or from the intermediate cells. It is impossible to tell from which.

The Rosette Cells. — At the 64-cell stage these are four in number, lying between the cross cells and considerably elongated inward. (See Pl. XXXVII, Figs. 16, 17, and 18, and Text-Figs. 3 and 4.) Soon after the stage represented in Pl. XXXVII, Fig. 17, one of them, invariably the one of the A quadrant, comes to the surface and divides equally (Pl. XXXVII, Fig. 18, *ar*). Next, the one in the D quadrant divides (Pl. XXXVII, Fig. 20, *dr*). Later, the two remaining cells divide, and the resulting plate of eight cells is shown with stippled nuclei in Pl. XXXVII, Figs. 22 and 23. These cells differ so little in size from those around them that the two are hard to distinguish, but I think the arrangement given in Pl. XXXVII, Fig. 23, is correct. The cells elongate slightly inward (Text-Figs. 5 and 6, *ar*). From them arises the tuft of apical cilia which from now on is a prominent feature of the larva. I think that all of the eight cells become ciliated.

The Second Quartette. — At the 64-cell stage there are sixteen of these cells, four in each quadrant, and a difference between the quadrants has shown itself by the peculiar division of one cell, leading to the formation of $X_{1.2}$, already mentioned. Since the fate of the second group of micromeres in the dorsal quadrant is different from that in the others, it will be advantageous to consider it by itself, and turn first to the second quartette in quadrants A, B, and C.

The first division concerns the upper dextral and lower sinistral cell (Pl. XXXVIII, Fig. 29). This is followed somewhat later by a division of the upper sinistral and lower dextral cells (Pl. XXXIX, Fig. 37). These divisions follow the law of alternation of cleavages only in the dextral cells, the sinistral dividing in precisely the same direction as their preceding division. Neither can the divisions be called bilateral, since the cells are not bilaterally arranged; and, indeed, from the 64-cell stage on, while some of the divisions of cells which lie near the median plane may be bilateral, the majority are not. They develop so as to produce in the end an embryo with bilaterally symmetrical organs; but data concerning the precise direction of each spindle, except in so far as they bear on the identification of cells, seem to me of little value. Cleavages may follow the law of alternation, or they may not, and neither case in itself is of any importance. The divisions of the dextral cells are of interest, for by them are produced three cells, which correspond to the "secondary trochoblasts" of Amphitrite, the cells $2a_{1.1.1}$, $2a_{1.1.2}$, $2a_{1.2.1}$, etc. (Pl. XXXIX, Fig. 38). In Amphitrite, however, the division of the upper cell is equal, while in Podarke it is very unequal (Pl. XXXIX, Figs. 37 and 38).

In each quadrant, then, there are three cells, two large and one small, corresponding in origin to the secondary trochoblasts of Amphitrite. (See Pl. XXXIX, Figs. 37, 38, 41, etc., ap_1''', ap_2''', $2a_{1.1.1}$, bp_1''', bp_2''', $2b_{1.1.1}$, cp_1''', cp_2''', $2c_{1.1.1}$.) Fig. 56 (Pl. XL) shows the relation of these cells to the rest of the prototroch: cp_1''', cp_2''', $2c_{1.1.1}$. While, however, $2c_{1.1.1}$, and $2c_{1.1.2}$ (cp_1''' and cp_2''') have elongated considerably, their nuclei have become swollen and contain prominent nucleoli, and the whole cell stains with difficulty, — agreeing in this respect with the cells of the primary prototroch, — the small cell $2c_{1.1.1}$ remains very small and with a very deeply staining nucleus. Later, as a result of the shifting of cell areas, this small cell is shoved out of the prototroch ring, and, I believe, forms a part of the ectoderm of the subumbrella, though its later history is difficult to follow. This process occurs in all three quadrants. Compare Pl. XL, Fig. 56, an embryo of 12 hours 35 minutes, with Pl. XXXIX, Fig. 48, an embryo of 24 hours ($2b_{1.1.1}$ and $2c_{1.1.1}$). These figures show two stages in the shoving of this small cell out of the prototroch ring. Later embryos show it lying entirely below the prototroch. The other two cells form a part of the completed prototroch, though they acquire their cilia very late. In the stage represented in Pl. XXXIX, Fig. 48, they are still without cilia. A little later they push up into the prototroch ring and all the cells elongate still more, this latter process coinciding with the closure of the dorsal interruption. They stain very poorly, so that their outlines are impossible to follow in later stages.

The other divisions of the second quartette are as indicated in Pl. XXXVIII, Fig. 36; Pl. XXXIX, Figs. 41, 42, 46; Pl. XL, Figs. 50, 51; and in the table, p. 438.[1] One cell is, however, of especial interest. This is the cell $2b_{2.2.1}$ shown in Pl. XXXIX, Fig. 41. Here it is seen at some distance from the edge of the blastopore. It divides once only. (See the products of the division in Pl. XL, Fig. 51.) While the corresponding cell in quadrant A divides vertically and equally (Pl. XXXIX, Fig. 41), this division is horizontal and unequal, a small cell being budded off dorsally. The ventral product, $2b_{2.2.1.2}$, does not divide again at the surface. Gradually the cells between it and the blastopore, — descendants of $2b_{2.2.1}$, — invaginate to form a part of the stomodaeum, and this cell, $2b_{2.2.1.2}$, approaches closer and closer to the blastoporic margin, and finally invaginates. (See Pl. XXXIX, Figs. 43, 44; Pl. XL, Figs. 49, 50, 51, 52, 54, 55.) In the stage represented in Pl. XXXIX, Fig. 47, it lies underneath the surface in the wall of the stomodaeum, where its nucleus is indicated by the dotted line. It later divides, but I have not been able to follow its subsequent history farther than to say that it forms a part of the stomodaeal wall.

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[1] In Pl. XXXIX, Fig. 46, I have indicated by the numeral on each cell the share which the second and third quartettes take in the composition of the ventral ectoderm.

The history of the second quartette cells in the dorsal quadrant is of especial interest for purposes of comparison, since in many annelids and mollusks they give rise to a large part or all of the ectoderm of the body, and in Amphitrite and Arenicola, at least, the paratroch of the larva is formed from descendants of this group. I shall follow Wilson and Mead in giving to these cells the especial name "X." For the sake of clearness I have enclosed the X-cells in a heavy outline.

The first divisions of X have already been described, the small $X_{1.2}$ arising in the 64-cell stage. (See Pl. XXXVIII, Fig. 26, where I have labelled the figure to correspond with Mead's nomenclature for the X-cells.) The next divisions occur in $X_{1.1}$ and X_2 (Pl. XXXVIII, Fig. 30, and Pl. XXXIX, Fig. 39), and these are soon followed by a division of X_3 (Pl. XXXVIII, Figs. 31 and 32), where the completion of this division is shown. $X_{1.1.1}$ next divides (Pl. XXXIX, Fig. 39), and there results a larger cell above, $X_{1.1.1.1}$, and a smaller, $X_{1.1.1.2}$, below (Pl. XXXIX, Fig. 40). At nearly the same time $X_{1.2}$ divides (Pl. XXXVIII, Fig. 35, and Pl. XXXIX, Fig. 39). In Pl. XXXIX, Fig. 40, is shown the division of $X_{2.1}$, and $X_{2.2}$, and $X_{1.1.2}$. Pl. XXXIX, Fig. 42, shows the division completed. $X_{1.1.1.1}$ next divides and at about the same time division occurs in $X_{2.1.1}$. These divisions are shown as completed in Pl. XXXIX, Fig. 42. These cells with their descendants now become difficult to distinguish from the cells of the third quartette near them, and as nothing of importance was to be gained from such a study, I have not attempted to carry them farther. $X_{1.1.2.1}$ and $X_{1.1.2.2}$ next divide equally (Pl. XXXIX, Fig. 43), and $X_{2.2.1}$ (Pl. XXXIX, Fig. 44), very unequally, the latter budding off a small cell to the left of

$X_{2.2.2}$. Later, $X_{1.1.2.1.1}$ and $X_{1.1.2.1.2}$ divide very unequally, each budding off a small cell downward, and at the same time $X_{3.1}$ sends a small bud upward (Pl. XXXIX, Fig. 45, and Pl. XL, Fig. 53). These small cells, formed from $X_{3.1}$ and $X_{1.1.2.1.1}$, have very deeply staining nuclei, and are excellent landmarks. The general rotation, which all the dorsal cells undergo, affects these latter cells so that the small cell, $X_{1.1.2.1.1.2}$, comes to lie underneath $X_{3.2}$, while its sister-cell lies to its right (Pl. XXXIX, Fig. 48). Meanwhile the small cell, $X_{1.2.2}$, has migrated inward, and forms a part of the wall of the proctodaeum, while its sister-cell lies at the edge of the blastopore. This afterwards divides again (Pl. XXXIX, Fig. 46).

As a result of the divisions described above, the condition of the X-group is as shown in Pl. XXXIX, Fig. 47. At the dorsal edge of the blastopore are three cells, one of which is dividing. $X_{2.2.2}$ divides next, unequally and in a meridional direction. The smaller product lies to the outside, and later $X_{1.1.2.2.1}$ buds off a small cell dorsally, which lies just below $X_{3.2}$. These cells occupy this position for some time, but subsequently divide, and the ventral edge of the X-group is composed entirely of small cells. (See Pl. XL, Fig. 59.)

In Pl. XXXIX, Fig. 47, $X_{3.2}$ is shown very much flattened and elongated, having remained undivided from the stage shown in Pl. XXXIX, Fig. 39. Together with the ectoderm cells which have migrated from the upper hemisphere, it has become excessively thin and transparent, but can always be recognized by means of its large vesicular nucleus and prominent nucleolus (Pl. XL, Fig. 57). As already stated, it and the "l_1" cell just above it are excellent landmarks in following the shiftings of position which the dorsal ectoderm cells undergo. Finally l_1 divides, and immediately afterwards $X_{3.2}$ divides bilaterally. Pl. XL, Fig. 58, shows the spindle of this division with the products of the division of l_1 lying just above it on either side. The daughter-cells of $X_{3.2}$ elongate considerably, and push apart (Pl. XL, Fig. 59). They may be recognized in later stages lying in this position, one on either side of and dorsal to the protodaeum. Each soon buds off a small cell downward and outward. In a considerably later stage I have seen, occupying the position of these cells on either side, a row of two or three small cells, which apparently have come from a division of $X_{3.2.1+}$ and $X_{3.2.2+}$, but I am unable to give any positive statements about their origin or destiny. They have an appearance which strongly suggests teloblasts, but I do not know if they have that character. Indeed, the cells $X_{3.2.1}$ and $X_{3.2.2}$ (Pl. XL, Fig. 59) look very like teloblasts, but if they are their teloblastic growth must begin much later, for none of the ectoderm anterior to them has, in the stage figured, come from their division. Their later position also resembles very much that of the paratroch cells figured by Mead (No. 22) in Amphitrite, but in the latest stages I have seen no cilia are found on them.

I have described these divisions of the X-cells at some length because of their value for purposes of comparison with other annelids. Amphitrite and Arenicola (No. 4) are the only annelids where the exact origin of the paratroch is known. Podarke, as said before, probably has no paratroch, but so important an organ might, on one theory of cleavage, be supposed to be present as an ancestral rudiment; and I was interested to follow the cleavages in the three genera to see if any similarities appear. The divisions of the X-cells in Podarke beyond the stage of Pl. XXXVIII, Fig. 30, have no similarities whatever to those of Amphitrite (No. 22) nor to those of Arenicola, as I learn from a comparison with figures kindly given me by Dr. Child.

I have already spoken of the way the dorsal ectoderm cells flatten out and spread apart. It is as if the cells from the upper hemisphere spread out like a fan, with their center near the upper edge of $X_{3.2}$, and carried the X-cells with them around towards the ventral side. The direction in which the forces which produced this shifting must have acted is shown in Pl. XL, Fig. 59, by the elongated cells $X_{3.2.1}$ and $X_{3.2.2}$.

The break in the prototroch remains open much later than in Amphitrite, and is represented as just closing in Pl. XL, Fig. 58. Whether or not this be regarded as the cause, the result is that a much larger portion of subumbrellar ectoderm comes from these cells than from the corresponding cells in Amphitrite. In fact, *a very limited portion of the subumbrella is formed from the* X-*cells*, as is shown in Pl. XXXIX, Fig. 48; Pl. XL, Figs. 58 and 59. To this point, which is mainly of importance in a discussion of homologies, I shall return. (See p. 467.)

As a result of this migration and expansion of the dorsal ectoderm cells, the X-group are forced ventrally and finally concresce on the ventral surface (Pl. XXXIX, Figs, 46–48). I am not absolutely certain that some of the cells figured as lying just outside the X-group may not really belong to the latter. The descendants of the third group of micromeres lie close to the X-group on either side, and so many shiftings occur that it is impossible to follow every cell. For our present purpose the precise history of every cell is not absolutely necessary. The point of importance is that the X-cells surround the proctodaeum and, if it be safe to rely on analogy, make up the budding zone of the larva. I have thus far been unable to rear larvae, though they will live in confinement for as many as ten days. Probably connected with the lack of proper food (for the small amount of yolk in the egg must be rapidly used up) is an exceedingly slow rate of development during the time that they will live in captivity. Similar difficulties with other annelids have been described by Hatschek (No. 11) in Eupomatus, von Drasche (No. 7) in Pomatoceros, and Mead (No. 22) in Lepidonotus. Beyond a slight increase in length, practically no growth takes place after the second day. In Amphitrite, Mead has proved that all of the body behind the first segment arises from descendants of 2d. For reasons above mentioned, I am unable to make any positive statements about their fate in Podarke, but in view of their position I think the presumption is strong that here also the body ectoderm arises from 2d.

Of interest in this history of the X-cells in Podarke is the fact that their divisions are not bilateral, so that until at least a very late stage the cells are not symmetrically placed with regard to the sagittal plane. Pl. XXXIX, Fig. 46, for example, shows a marked asymmetry. This asymmetry is partly due to asymmetrical divisions, and partly due to shiftings of positions which the cells undergo. In Pl. XXXIX, Fig. 42, for example, the cells $X_{1.1.1.1}$ and $X_{2.1.1}$ are seen to lie close against the prototroch cells in C and D quadrants respectively. Just to the left of $X_{2.1.1}$ are two small cells, $2a_{2.1.1}$ and $2a_{2.1.2}$ (Pl. XXXIX, Fig. 43). When the cell areas shift so that the prototroch cells take their final position, I believe that the cell $2a_{2.1.1}$ is pushed up between $X_{2.1.1}+$ and the prototroch (Pl. XXXIX, Figs. 44 and 45), while, on the other hand, the cell $X_{1.1.11.}+$ is pushed up between the prototroch cells (Pl. XXXIX, Fig. 45; Pl. XL, Fig. 56). The result of this movement is that on the left side the X-cells occupy a broader area, when seen from below (Pl. XXXIX, Fig. 48), than do those of the right of the median plane. In much later stages (Pl. XL, Figs. 57 and 58) a small cell lies wedged in between the cells of the prototroch in the C quadrant. This cell, I believe, is a descendant of $X_{1.1.1.1}$, which has been separated from the X-group by the migrating cells from the upper hemisphere. In later stages the large $X_{3.2}$ divides symmetrically (Pl. XL, Fig. 58), but I have been able to discover no other symmetrical divisions. Neither could I find any divisions, such as Mead has described in Amphitrite, which, though themselves asymmetrical, had direct reference to the symmetry of the trochophore.

The Third Quartette.—At the 64-cell stage these are eight in number, two in each quadrant. We have already seen that the next division establishes bilateral symmetry at the upper pole. Symmetry also appears at the same time at the lower pole as a result of the peculiar division of two of the third group and one of the fourth. Leaving the latter for the present with merely the remark that it is 4d and contains the mesoderm, let us notice the division of the third quartette cells (Pl. XXXVIII, Figs. 26 and 27). Here $3d_2$ and $3c_2$, lying one on either side of 4d, are dividing in a bilaterally symmetrical fashion. (The second line of cleavage in the specimen from which Pl. XXXVIII, Fig. 27, was drawn had changed its direction. This is rare in this stage and I have never found it in earlier stages before $X_{1.2}$ is formed.) The outer product of the division in both cases is the smaller and may be neglected in the further description. The inner products show from the first a tendency to invaginate (see Pl. XXXVIII, Fig. 28), where their nuclei lie beneath the surface. Later each cell divides dorsally a small cell, coming to the surface to divide (Pl. XXXVIII, Figs. 35, $3d_{2.1}$ and $3d_{2.2}$, and 36, $3c_{2.1.2}$ and $3d_{2.2.2}$). Their nuclei immediately start to invaginate again. Finally each nucleus comes to the surface and a very small cell is budded off (Pl. XL, Figs. 50 and 51), and all four of the cells thus formed invaginate to give rise to a large part of the *larval mesoblast,* which is entirely the functional mesoblast of the larva. As we shall see immediately, the larval mesoblast is completed by the addition of other cells from another quadrant.

Of the other products of 3d and 3c little need be said; $3d_1$ and $3c_1$ divide meridionally soon after the first division of $3d_2$ and $3c_2$ (Pl. XXXVIII, Fig. 28, $3d_1$), and a number of later divisions have been noted. (See Pl. XXXIX, Figs. 40, 42, 44, 46, and table, p. 438.) They form a portion of the ventral ectoderm of the trochophore, take part in the closure of the blastopore, and make up a part of the proctodaeal wall. (See Pl. XXXIX, Fig. 46.)

The first division of the third group of micromeres in the A and B quadrants is shown in Pl. XXXVIII, Fig. 28, where $3a_2$ and $3b_2$ are dividing meridionally. A little later $3a_1$ and $3b_1$ divide also meridionally (Pl. XXXVIII, Figs. 34 and 35). The next division in A quadrant is of cell $3a_{2.2}$ (Pl. XXXIX, Fig. 41). This divides unequally, sending a small cell upward, $3a_{2.2.1}$ (Pl. XL, Fig. 50), while the larger lower portion begins to invaginate (Pl. XL, Figs. 50 and 51). This cell, $3a_{2.2.2}$, passes into the segmentation cavity and becomes *larval mesoblast.* Originally situated at the left of the median plane, it passes forward and lies directly in this plane. Its next division is equal. (See Pl. XL, Fig. 52, and Text-Fig. 7.) From this time on its products lie symmetrically on either side of the median plane. A corresponding cell in B quadrant divides at about the same time as this and apparently invaginates (Pl. XL, Figs. 49 and 51). I at first supposed that this also becomes *larval mesoblast.* Careful examination, however, fails to show any trace of this cell lying in the segmentation cavity, and all the larval mesoblast of the anterior end of the body, as is unmistakably shown by the specimens, comes from the cell $3a_{2.2.2}$. I have been unable to trace the cell $3b_{2.2.2}$ with any accuracy after the stage shown in Pl. XL, Fig. 51, but from its position I suppose that it aids in the formation of the stomodaeum. The entoderm cells have divided repeatedly, and at this time are no larger than the cells at the edge of the blastopore, so that it is difficult to distinguish between the two sets.

The further history of the other descendants of 3a and 3b, so far as I have followed it, is given in Pl. XXXIX, Figs. 46 and 47, and in the table, p. 438. Detailed description would be profitless. They form a part of the stomodaeum and the general ectoderm of the subumbrella.

Larval Mesoblast.

This arises in Podarke, as we have seen, from descendants of 3d, 3c, and 3a. The two former are symmetrically arranged from the beginning, while the latter only become so placed after invagination and division. It is important to note that this division, which occurs in $3a_{2.2.2}$, *after* its invagination, corresponds to the division which in the other cells gave rise to the small cell ventrally, and which takes place at the surface. In both cases both products of the division become mesoblast, so that all the cells of the larval mesoblast belong to the same generation. I have indicated these cells as *right, l.m.r., left, l.m.l.,* and *median, l.m.m.* After the next division, immediately to be described, the smaller product of the posterior larval mesoblast, when seen from the side, lies over the large $4d_2$ cells (Pl. XL, Fig. 56), while the others have spread farther apart in the cleavage cavity.

The larger products of the posterior larval mesoblast divide next, and there is formed a band of three cells on either side of the median line (Pl. XL, Figs. 52 and 54, and Text-Fig. 7). Since the posterior end of each band lies very close to the definitive mesoblast (colored a deeper pink in the figures), the effect is that of two well-developed mesoblast bands, lying in the usual position in the segmentation cavity, and they would undoubtedly be described as such by any one who saw merely the preparation figured in Pl. XL, Fig. 54. Very soon, however, the larval mesoblast cells begin to migrate (Pl. XL, Figs. 53, 55, 56). In Pl. XL, Fig. 56, is shown the position of the posterior larval mesoblast, while the anterior, at this stage, is composed of four cells on a side. The cells elongate and become the larval musculature. They are especially well developed in the region of the prototroch, under which the long, spindle-shaped cells may easily be recognized in later stages. (See Text-Fig. 8.)

Comparative. — A larval mesoblast was first discovered by Lillie (No. 21) in Unio, where it arises asymmetrically in the A quadrant only, from the second group of micromeres, $2a_2+$. This migrates so as to lie symmetrically in the cleavage cavity, and by its division are formed cells which become metamorphosed into the "myocites" and larval adductor muscles, which are functional only during larval life. Later Conklin (No. 5, *a*), in Crepidula, found larval mesoblast arising from the second quartette in three quadrants, A, B, and C. In the left-wound gasteropods, Physa and Planorbis, which have the "reversed" type of cleavage, Wierzejksi (No. 31) and Holmes (No. 15, *b*) found it arising from the third quartette in B and C quadrants; in these reversed cleavages, therefore, symmetrically arranged. In annelids, thus far, the structure in question has been found only in Aricia, Capitella, and Podarke. In Aricia, Wilson (No. 34, *g*) finds two cells arising symmetrically from either the second or third quartette. Through lack of material he was unable to discover its exact origin. In Capitella, Eisig (No. 8) finds it arising from the ventral products of the second division of 4d, thus corresponding in origin to cells which in other annelids become entoderm. (See p. 451.) To this point I shall return later.

From the figures which Hatschek gives for Eupomatus, it seems to me extremely probable that a larval mesoblast is present there also, although the point is not one to which Hatschek paid any attention. His figures (Pl. XXXIX, Fig. 42 to Pl. XL, Fig. 49) show scattered muscle cells in the upper hemisphere of the larva, which could hardly have come from the feebly developed mesoderm bands at the posterior end of the body. The same suggestion would apply to Pomatoceros, as described by von Drasche (No. 7), where Pl. XXXVII, Fig. 20, shows a muscle cell just underneath the apical pole, and the small compact mass of seven mesoblast cells, showing no trace of differentiation, quite at the other end of the larva.

The cell origin of the larval mesoblast in the forms where it has been thus far described is as follows :

Unio	$2a_{2\cdot1}$ +.
Crepidula	2a, 2b, 2c.
Physa	3b, 3c.
Planorbis	3b, 3c.
Aricia	2nd or 3rd quartette.
Capitella	$4d_{2\cdot2}$, $4d_{1\cdot2}$.[1]
Podarke	$3a_{2\cdot2\cdot2}$, $3c_{2\cdot1\cdot2}$, $3d_{2\cdot2\cdot2}$.

Fourth Quartette. — At the 64-cell stage the fourth group of micromeres has just been formed, and, so far as one can tell with the microscope, are all exactly alike. Very soon, however, as we have seen, one of the cells divides bilaterally, thus aiding in the establishment of the bilateral symmetry of the body. These cells, like those of the third quartette just adjoining them, early show a tendency to invaginate, and they divide at the same time as the latter, each budding off ventrally and posteriorly a very small cell (Pl. XL, Fig. 51). The two then invaginate and can be seen through the transparent X-cells lying just underneath the surface. It is important to notice, however, that at the same time that these cells invaginate a gastrulation begins, and the entoderm cells push in at the same time as the cells $4d_1$ and $4d_2$. (Since until the stage of Pl. XL, Fig. 57, the mesoderm is not fully differentiated, I have retained the designation $4d_1$, etc., for the descendants of 4d in the earlier figures. The small cells which enter into the archenteric wall I have indicated by *en* in Pl. XL, Figs. 51–57.) This accounts for the fact that the descendants of 4d undergo such extensive shiftings of position without at the same time losing their connection with the wall of the archenteron. The two small cells described as budded posteriorly from $4d_1$ and $4d_2$ form a part of the wall of the archenteron. Since the greater part of 4d gives rise to the definitive mesoblast, it is therefore, to use Conklin's term, a mesentoblast cell.

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[1] Here, as elsewhere in the comparative portion of this paper, I have modified the nomenclature to conform with that adopted for Podarke. (See also p. 465.)

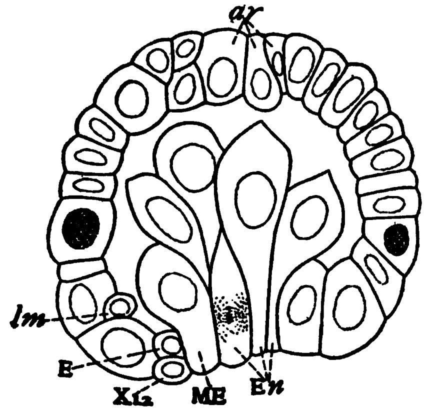

FIG. 5.—Beginning of entodermal invagination. *En*, entoderm; *lm*, larval mesoblast; *ME*, 4d before the final separation of mesoderm from entoderm; *E*, the first entoderm cell budded off from $4d_2$. $X_{1.2}$. the "anal" cell.

The cells $4d_{1.1}$ and $4d_{2.1}$ at first lie in the wall of the archenteron, though they protrude considerably into the segmentation cavity. Consequently, in a section passing a little to one side of the sagittal plane, they seem to lie wholly in this cavity (Text-Fig. 6). Each buds off a second small cell (Pl. XL, Fig. 56), and the larger portion is the definitive mesoblast, M_1 and M_2. Considerably later (Fig. 57, Pl. XL, and Text-Fig. 8) each divides equally. Only until this last division do these cells entirely lose their connection with the archenteric wall. Text-Fig. 8 is an optical section of the specimen drawn in Fig. 57, and shows that the descendants of 4d are still connected with the entoderm. I have actual sections of this stage which show exactly the same thing. The products of the last division migrate rapidly through the segmentation cavity, retaining approximately their original

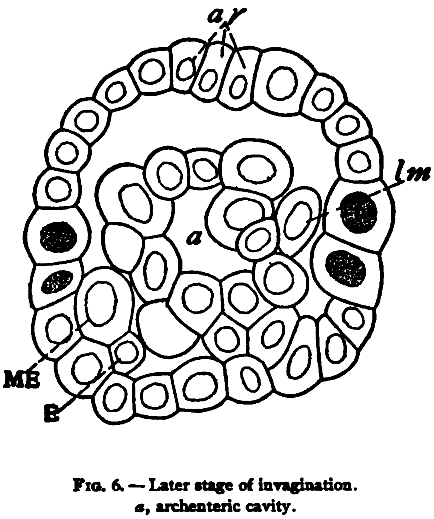

FIG. 6.—Later stage of invagination. *a*, archenteric cavity.

direction, at right angles to the prototroch, and eventually lie on either side the ventral surface, just underneath the adoral zone of cilia (Pl. XL, Fig. 59). This is the latest stage to which I have carried the mesoderm cells in what I am positive were normal embryos. In older embryos I have found a large pole cell occupying a position like the posterior one of the two cells figured in Fig. 59, while a row of small cells extended anteriorly from it. The difficulties experienced in getting larvae to develop after the third day have as yet prevented me from securing any complete details of the later history of these cells, and since the study of the trochophore development has been taken up by another worker, I have thought it best to leave the subject at this point. In calling these cells the germ bands, I am not relying entirely on analogy with other annelids, although the resemblance is close, but on the fact that both ectoderm and entoderm are fully differentiated at this stage, and these cells, lying in the segmentation cavity, are the only source from

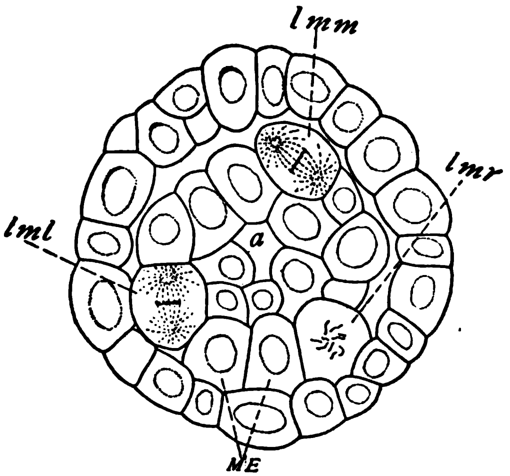

FIG. 7. — Horizontal optical section through Fig. 52, Pl. XL, taken at level of larval mesoblast. *lmr, lml, lmm*, right, left, and median larval mesoblast. Other letters as before.

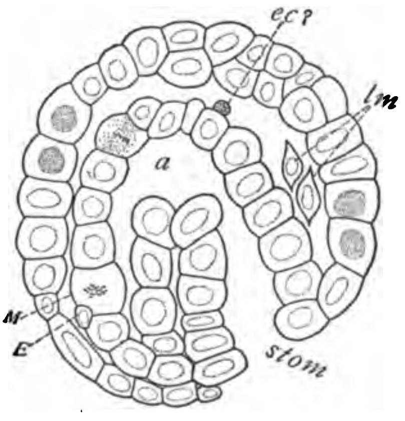

FIG. 8. — Sagittal section through stage of Fig. 57, Pl. XL. *ec*, ectodermal cell; *M*, definitive mesoblast, in its first division after eliminating all the entodermal elements; *stom*, stomodaeum.

which mesoderm can arise, unless we assume an ectodermal origin, which is not probable. Hence I have no hesitation in saying positively that they are the germ bands.

The second pair of small cells, like the first, enter into the wall of the archenteron.

Comparative. — In all annelids, gasteropods, and lamellibranchs thus far studied, with one exception, the definitive mesoblast arises from 4d. The exception is Capitella, where, according to Eisig, 4d contains only a little larval mesoblast, while the greater part of the cell is ectodermal and enters into the ventral plate. The definitive mesoblast in this form arises from 3c and 3d. (See p. 451.) In Nereis, Wilson (No. 34, *d*) described small cells budded off ventrally from $4d_1$ and $4d_2$, which he at first called "secondary mesoblast," and supposed they lay on the dorsal wall of the archenteron. In Aricia only one of these cells appears on either side. Later, however, Wilson has shown (No. 34, *g*) that the so-called secondary mesoderm cells do not form mesoderm at all, but really become a part of the wall of the archenteron. In Amphitrite (No. 22), Polymnia[1] (No. 34, *d*), and Arenicola (No. 4) this entodermal portion is lacking in the cell 4d. In Amphitrite, Mead described a very small cell at the anterior end of the germ band, which he suggests may be a reminiscence of the superficial budding which takes place at the surface in other forms, and Wilson has definitely homologized the two sets of cells. Inasmuch, however, as these cells always remain in the mesoderm, such a comparison seems to me doubtful, and, if *vestigial at all*, they represent rather some mesodermal structure. As I have pointed out on p. 472, the small size of cells when first formed is no proof of their vestigial character, since they may subsequently undergo any amount of growth. In Clymenella, Mead (No. 22) described the first division of $4d_1$ and $4d_2$ as equal instead of the very unequal division of Nereis or Aricia. Wilson (No. 34, *g*) has suggested that the posterior portion of each of these cells is entoderm. While this is possible, it has not been proved, and hence the structure is of little value for comparison.

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[1] See, however, Wilson (No. 34, *g*), p. 12 of reprint.

Among the mollusks Conklin (No. 5, *a*) has shown that 4d in Crepidula is more than half entoderm. It is not impossible that a portion of this cell in Unio may have a similar fate, and a close relation between mesoderm and entoderm has been described for Cyclas (No. 28) and Patella (No. 26), though the precise cell origin of the mesentoblasts in the latter cases was not determined. These observations seem to indicate a lack of uniformity in the mode of origin of the mesoblast and also show an *apparently* close relation between mesoblast and entoblast. To this point I shall return later. (See p. 449.)

The other members of the fourth quartette apparently invaginate. (See their small superficial area in Pl. XXXVIII, Figs. 33 and 35.) In Pl. XXXVIII, Fig. 34, the nucleus of 4a shows underneath the 2a cells. In some cases I was unable, in the stained specimens, to see the outlines of the cells. This fact led me to the erroneous statement in my preliminary paper (No. 29, *a*) that they invaginate before dividing. As a matter of fact, the cells come to the surface and divide equally (Pl. XXXVIII, Fig. 36), and then immediately invaginate, entering into the wall of the archenteron.

The Fifth Quartette. — A fifth series of four cells arising from the entomeres has been called the fifth quartette of micromeres by other workers, and in my preliminary note (No. 29, *a*) I emphasized the fact that in Lepidonotus, as in Podarke, such a quartette appears. The term, however, is misleading, since the cells thus formed are entodermal in destiny; and we must regard this division as corresponding to the division which, in other forms, takes place after invagination. The only difference between the two cleavages is that one takes place at the surface and the other below it. The one is as truly a fifth quartette of micromeres as the other.

This division in Podarke is shown in Pl. XXXVIII, Fig. 33, occurring in C and D quadrants, and later it appears in quadrants A and B (Pl. XXXVIII, Fig. 34). The eight cells thus formed, together with six derived from the division of three members of the fourth quartette, make up an invaginating plate of fourteen cells, which rapidly invaginates, its cells meanwhile dividing again; and the alimentary canal of the embryo is quickly mapped out. The details of this process I am unable to give, for it is impossible on surface views to see the outlines of the cells; and on account of the small size of the embryos, sections are very unsatisfactory objects for study, the difficulties in the way of accurate orientation being too great. I can only say that the alimentary canal is rapidly formed, being practically completed by the twenty-third hour of development. As in Nereis (Nos. 34, *d* and *g*), the posterior ectoderm cells bud off some small cells, which enter into close relations with the entodermal portion of 4d. Some stages in the invagination and hollowing out of entoderm cells are shown in Text-Figs. 5, 6, 7, and 8.

The stomodaeum, as already stated, is formed by cells from both the second and third quartettes. The invagination which some of these cells undergo is shown most clearly by the aid of the landmark furnished by the cells $2b_{2.2.1.2}$. already described on p. 420. The anterior portion of the blastopore becomes the mouth, and its sides are closed by cells from both the second and third quartettes. The proctodaeum arises at the posterior end of the blastopore, which I do not believe ever completely closes. Thus both mouth and anus arise from it (*cf.* Conn, No. 6). The cell $X_{1.2.2}$, as already stated, early invaginates to form a part of the proctodaeal wall, but the exact origin of the other cells which invaginate I was unable to determine. From their position in earlier stages, I believe that the cells $3c_{2+}$ and $3d_{2+}$ are the ones most deeply concerned, but the small size of the cells and the shiftings of position which they undergo make it impossible to be certain. (See Pl. XXXIX, Fig. 46.)

The trochophore is now fully formed. The apical tuft of cilia still remains at the anterior end of the umbrella, and about midway between this and the prototroch is a second tuft. (See Pl. XL, Fig. 60.) The prototroch is now a complete ring, the origin of its cells having already been described. An adoral zone of cilia extends from the mouth to the anus ("Neurotrochoid" of Eisig), but no paratroch is present. On the ventral surface of the umbrella are the two orange-colored "eye-spots," and the large clear spaces, which are undoubtedly similar in origin and function to the "frontal bodies" of Nereis and the "problematic bodies" of Amphitrite. In Nereis, Wilson supposes each to arise from a single cell, which becomes vacuolated and probably has a glandular function. In Podarke there are two on a side, closely crowded together just in front of the eyespot, and a fifth very small one on the median line in front. They stain very deeply with haematoxylin, an outer portion (Wilson's "duct") staining much more deeply than the inner. From the number of nuclei surrounding each "body" in the early stages, I think they are formed from more than one cell. Their staining reactions indicate that they have a glandular function, and they are apparently the only glands in the body. In the case of these glands, as well as in that of the so-called "slime glands" in other annelids, I agree with Eisig (No. 8), that they probably have an excretory rather than a slime secreting function, the necessity for the one and not for the other being apparent.

A marked feature of the larva of thirty hours and later is a circular shelf, which extends around the cavity of the archenteron and, when seen from the side, apparently divides it into distinct compartments (Pl. XL, Fig. 60). Careful observation shows, however, that this is really a broad, very thin shelf of tissue. The opening through it is at first at the center of the ectoderm cavity; later it lies at the dorsal side of the enteron. Just above it is a tuft of long cilia, a modification of the general ciliation of the archenteron. (See Pl. XL, Fig. 60.) The first appearance of this structure is at about twenty-three hours, when a slight constriction appears at about the middle of the archenteron. Partly by the swelling out of the archenteron above and below it, and partly by an active growth of the cells involved, is formed a circular shelf of tissue extending out into the cavity of the alimentary canal. In embryos of about thirty hours, if the specimen be rolled so that the proctodaeum looks upward, careful focusing through the proctodaeal opening shows this circular shelf running entirely around the archenteron, and extending about one-half the way across its cavity. The organ at this stage bears a very striking resemblance to the velum of a medusa. Later it becomes very thin and vacuolated, and the details of its structure are difficult to make out. The original opening, as I believe, moves backward to the position described above, and I think other openings break through it, but of this I am not certain. When first formed, the partition is ciliated above and below. I do not know how long that condition lasts. (See Pl. XL, Fig. 60.) The section passed a little to one side of the central opening, which therefore does not show in the drawing.

The suggestion has been made that this partition represents the first septum, but I do not believe that is so. So far as I can discover, only entoderm cells enter into it. It seems to me rather to lie at the boundary line between "stomach" and "intestine" of the larva, and to be merely an exaggeration of the constriction found at that point in other annelid larvae. (See No. 7, Pl. XXXVIII, Fig. 26.)

As already stated on p. 435, the wall of the archenteron swells out so as to lie close under the ectoderm. Since dorsally both layers are very thin and transparent, it becomes difficult, on surface views, to make out the outlines of the cells. Indeed, it frequently is impossible, except by rolling the specimen so as to get an optical section, to determine to which layer a given nucleus belongs. Ventrally (Pl. XL, Fig. 60), the ectoderm is much thicker.

At this point the cell lineage naturally ends, and the study of the trochophore begins. Since the problems of the latter subject are so different from those of the former, it has seemed best to reserve the metamorphosis of the trochophore for another paper.

Comparison with other Annelids having "equal" Cleavage. — The most complete account of the cleavage of an equally segmenting annelid previously published is that of Mead (No. 22) on Lepidonotus. To Dr. Mead's generosity I have been indebted for preparations of the later stages. A few observations have also been made on the cleavage of *Hydroides dianthus* and *Sthenolais picta,* both of which resemble Podarke in their mode of cleavage. I have not as yet carried the development of these forms far enough to justify a detailed account of the process, but enough has been seen to show as I pointed out in a preliminary paper (No. 29, *a*) that bilateral symmetry appears at practically the same time here as in Podarke, and that there is as much differentiation in the ovum as in any annelid with the unequal type of segmentation. The theoretical bearings of this fact I shall discuss later.

Table of Cleavages.

I have followed all divisions up to about 140 cells; later than this only especial groups were followed. All of these divisions are indicated in the accompanying tables. The well-marked stages of the earlier cleavages are denoted by the numbers at the top of the column, but after eighty cells these numbers must be regarded as only approximate. Each table gives the divisions of a single quadrant and begins with the 4-cell stage. The direction of each division is indicated by the straight line / inclined to the right for a dexiotropic, to the left for a leiotropic, vertical for a meridional, and horizontal for a horizontal cleavage. If it be remembered that the line always has the direction of the boundary plane between the two cells, I think the table will be readily understood. When the products of a division are equal, that is indicated by the sign of equality. If unequal, by the sign of inequality, placed across the direction line. A plus (+) sign after a cell number indicates that it has been seen to divide again, but its divisions were not followed.

In all cases the daughter-cells resulting from a division are put in the column indicating the number of cells in the whole embryo immediately after the division of these cells. Thus, at the 16-cell stage, 2A divides dexiotropically and unequally, the larger cell lying below. At the completion of this division the whole embryo contains twenty-four cells. The smaller cell, 3a, does not divide again, until about forty cells, and when this division is completed the whole embryo contains fifty-six cells, etc.

PART II. GENERAL CONSIDERATIONS.

Axial Relations.

The axial relations of the first cleavage planes have been described above (p. 405). Those of the trochophore agree with Amphitrite. The mesoblast bands occupy from the first their definitive position at right angles to the prototroch. Although the X-cells, as in Nereis, occupy a final position much farther from the prototroch than they were at first, the cells between them and the prototroch have a very different origin from the cells in a similar position in Nereis, and I have seen no evidence for a shifting of the neural axis, such as has been described by Wilson (No. 34, *d*). The descendants of the $X_{3.2}$ group form a row of large cells across the body which look like teloblasts, but I have no evidence that they really have that function. (See p. 423.) I do not think that all of the ventral ectoderm of the trochophore arises from the X-cells. All the evidence indicates that some of the other second, and probably to a limited extent the third, quartette cells have this fate. (See Pl. XXXIX, Fig. 46.)

Types of Cleavage.

In Podarke, as in other annelids, and in gasteropods and lamellibranchs, two types of cleavage, the radial and the bilateral, have been distinguished, the former appearing first, and being gradually displaced by the latter as development proceeds. The subject has been thoroughly discussed by Wilson (No. 34, *d*), Mead (No. 22), and Conklin (Nos. 5, *a* and 5, *b*), and I need not go over the ground again. As I have said in another place (see p. 470), the most reasonable explanation of these cleavages to my mind is that they were primarily mechanical, and that morphogenetic processes have been secondarily moulded upon the primitive forms. The first of these causes leads to the radial or spiral divisions which appear first, and the second to the bilateral divisions which have a direct reference to the bilaterality of the future body. I agree perfectly with

50 | 150 and over.

1a1.1.2.1.2.1. +
1a1.1.2.1.2.2.

Ectoderm of umbrella.

+
+

1a1.1.2.2.2.1.1.
1a1.1.2.2.2.1.2

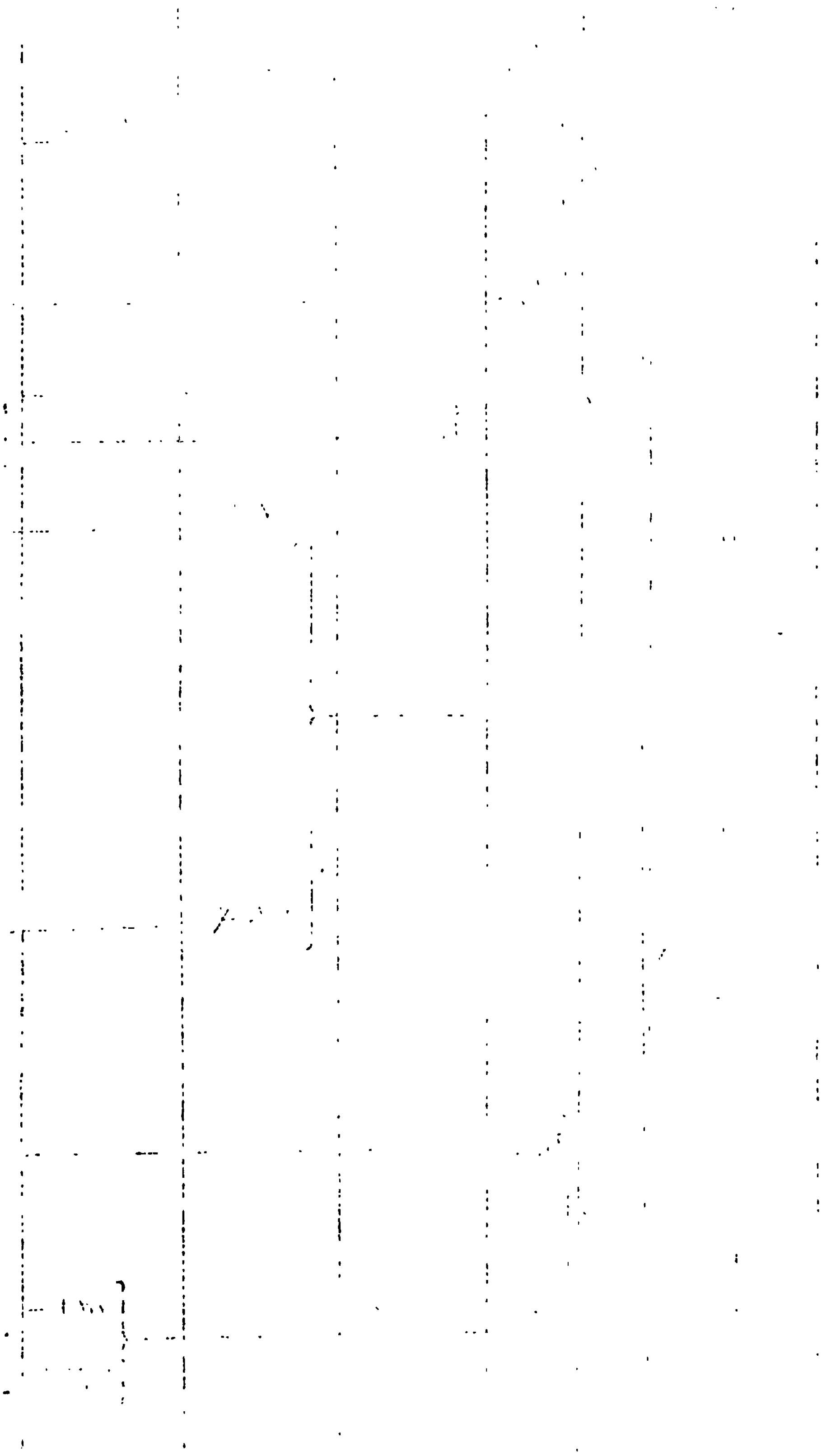
+

Ectoderm of subumbrella.

Stomodaeum wall.

Larval. mesoblast.

to 150	150 and over.
.1 .2. } rosette.	
.1. + .2. + .1. + .2. + } Ectoderm of umbrella.	
.1.1.+ ectoderm of subumbrella.	
1.2. .1. .. 2. } stomodaeal wall.	
a.	
— — — — — —	— 3b2.1.1. 3b2.1.2 } Ectoderm. and stomodaeum.



Conklin that both have become hereditary, which would explain their similarity in all these forms.

That the two types are not sharply separated but overlap is shown by the fact that the first indication of bilateral symmetry arises by a spiral cleavage, and is due to size differences of cells and not to any *reversed* direction of cleavage. (See Pl. XXXVII, Fig. 17.) Of value in this connection are the observations recorded on p. 415, showing cases of reversion to a radial type. The next divisions are bilateral (see Pl. XXXVIII, Fig. 27), showing divisions of $3c_2$ and $3d_2$. Hence in Podarke the transition is not the sudden one described for Nereis, but is gradual, as would be required by our hypothesis. Mead and Conklin have already pointed out the difficulties in the way of accepting Wilson's explanation of the cause for the time of appearance of bilateral symmetry, and to their conclusions I can add the facts in the development of Podarke, where bilaterality appears early, and no equalizing division is necessary for 2d.

The bilateral cleavages appear, as might be expected, at different times and in different ways in different animals. For example, in Crepidula, Conklin has shown that the primitive radial symmetry is preserved in the anterior quadrants after it has disappeared in the posterior ones, *e.g.*, the arms of the cross. In Podarke it is the cross which very early shows bilateral symmetry (see Pl. XXXVII, Fig. 17), so that the relation of bilateral cleavages solely to the processes which lead to the formation of the body is not as close here as in other forms (*cf.* Conklin, No. 5, *a*, p. 185). Indeed, I see no reason why they should, for, as I understand it, neither the trochophore nor its hypothetical ancestor, the trochozoön, has a radial, but rather a bilateral organization. The eye-spots, the glands, in short, *all* the structures of the annelid trochophore are bilateral and not radial. Hence the same causes which would transform the spiral cleavages into bilateral *body-forming* ones, would operate in producing the cleavages which lead to the formation of the *head.* What these causes are we do not know, other than that they must be mainly intrinsic.

Cell Mechanics.

In view of the number of observations which have been recorded by Mead (No. 22), Conklin (No. 5, *a*), Jennings (No. 16), Wheeler (No. 32), and others, showing that none of the laws of cell division, as formulated especially by Hertwig (No. 12), are of universal or even of general application, further additions to the list may seem superfluous, and I will mention but one case which shows that the karyokinetic spindle does not invariably lie with its long axis in the direction of greatest protoplasmic mass, or of least resistance. When the entoderm cells begin to invaginate, they become elongated, and their lower ends are very much compressed by the pressure of surrounding cells. (See Text-Fig. 5.) During this process the cells divide. Now it is evident that if division took place at right angles to the greatest elongation of the cell, or in the direction of greatest pressure, a two-layered entoderm would result. A two-layered entoderm would be of no especial use to the animal; what is needed is a larger area of absorptive surface, and that can only be obtained by a division in the opposite direction; in other words, in a direction such that the spindle lies in the line of greatest pressure, and at right angles to the greatest elongation of protoplasm. I have repeatedly seen spindles lying in these cells during the invagination process, and invariably they occupy the direction shown in Text-Fig. 5. Many other examples of this nature might be found in the cleavage of Podarke, emphasizing the fact that, as Conklin pointed out, protoplasm is "not soapsuds or oil emulsion," and that dominating the developing embryo is some force vastly more powerful in its influence on the embryo than any merely mechanical forces, and providing that every spindle shall take the direction necessary in order that a bilaterally symmetrical organism may result. If there is no especial reason why it should be otherwise, the spindle may lie in the long axis of the cell, or successive spindles may alternate in direction; but if in order that a perfect organism shall develop the spindles need to take some other position, that position will be assumed. Not only is this force manifest in the direction of divisions, but in the shifting of cell areas which occurs throughout the ontogeny. In an elaborate work on Ascaris, Zur Strassen (No. 36) has proposed a theory that attractions (cytotropisms) exist between groups of cells, and that these mutual attractions bring about the shifting of areas, which is a marked feature of the Ascaris embryo. Aside from the fact that there is no positive evidence of the presence of this cytotropism, the theory of Zur Strassen is hardly an explanation ; for, supposing that these attractions do exist (and no convincing evidence is given for their presence), their source and nature remain as mysterious as before. The fact cannot be too strongly emphasized that the embryo from the beginning is a complete organism, not a collection of more or less independent units, the "cells," and that controlling the whole development is some force the nature of which we do not know, but which provides that from a given ovum a given organism shall result.

Equal and Unequal Cleavage.

It has happened that most of the work on annelid cytogeny previously published has been done on annelids with the unequal type of cleavage, and the development of Podarke, therefore, is of especial interest as affording a means of comparison between the equal and unequal types. As we have seen, up to the 56-cell stage, all the quadrants of Podarke are alike, the only indication of a differentiation being the constant position of the polar furrow. Since the two ends of this furrow are, so far as we can tell with the microscope, alike, the possibility remains that they are *actually* alike, and that it is a matter for later determination whether one or the other shall be the posterior end. That this is not the case is, I think, shown by the regular appearance of definite organs at definite times and places in the later development. The small cell, $X_{1.2}$, appears first as an orientation point, and this is followed by the bilateral division of 4d and the regular series of events leading to the bilaterally symmetrical embryo. This indicates to my mind that the polarity of the ovum and of the early cleavage stages is as great as in any animal with the unequal type, even though this polarity may not be expressed so clearly in the form of cleavage. The alternatives to this position would be the theory that differentiation came in suddenly at the 64-cell stage, or that it, so to speak, accumulated very slowly, only attaining a visual importance at that stage. Of the three, I believe the first is correct. It is difficult to understand why closely related animals (or, for that matter, animals not closely related) should vary in the amount of polarity possessed by their ova at the beginning of development, and I believe a very different principle must be invoked to explain the difference. This question of differentiation in the trochophore of Lepidonotus, which also has an equal cleavage, has been discussed by Mead (No. 22, p. 278); and what he has said there applies equally well to Podarke. At the time Dr. Mead's paper was written there was still doubt whether the trochophore of Lepidonotus had a radial or a bilateral symmetry, inasmuch as the origin of the mesoblast was not known. As stated in a previous paper (No. 29, *a;* see also p. 436), there is no doubt that Lepidonotus has a bilaterally symmetrical cross and a small $X_{1.2}$ cell, exactly as in Podarke; and it is very probable that the history of the *definitive* mesoderm at least is essentially the same in Lepidonotus as in Podarke.

According to Mead, the important question to be settled by a study of equal cleavage is whether one of the two cells in equal is homologous with the larger in unequal cleavage. In the paper just cited, I have expressed my belief that it is. Later study has led me to somewhat different conclusions concerning homologies from those held by Professor Mead (see pp. 469); and to avoid misunderstanding it may be desirable to change the terminology, although the essential meaning remains the same. I believe that one area in the annelid with equal cleavage is homologous with a corresponding area in an annelid with unequal, and that there is as much differentiation in the one case as in the other, though, as I shall try to show later, the cells are probably not homologous.

What is the meaning of unequal cleavage? The old explanation was that it is due to the effects of yolk, either actually present or working through heredity. Rabl (No. 27, *b*), in his work on Planorbis, describes a series of mollusks in which at the 4-cell stage are found all gradations from four equal cells through others with an accumulation of yolk in three, then in two, and finally in one cell, the yolk-laden cells being larger than the others. From these observations Rabl argues that the primary cause of a difference in size among cleavage blastomeres is an accumulation of yolk in one cell, or a group of cells ; this mass of yolk causing the cell which contains it to be larger than the others. If a difference in size appears between micromeres above and macromeres below, it indicates that there is a good deal of yolk in the egg. If, on the other hand, this size difference appears in the 4-cell stage, there was not necessarily either more or less yolk involved, but its distribution is different. As far as I can discover, however, Rabl makes no attempt at explaining why yolk should have this unequal distribution.

If the problems of equal and unequal cleavage concerned only the first three divisions of the ovum, an explanation of this sort might suffice ; but the most superficial observation will show that it does not apply at all in later stages. Here cells of the same size develop equally or unequally, apparently without any reference whatever to the presence of yolk, and solely with reference to the needs of the developing embryo. Examples of this sort are numerous in the development of Podarke. At the 32-cell stage the cells at the upper pole are a very little larger than those at the lower, but at the next division the very small apical rosette cells appear at the upper pole, while at the lower the division is nearly equal. It cannot be maintained that there is more yolk in the cross cells than in the cells which later become entoderm. Again, the cell $2d_{2.2}$ certainly contains no more yolk than the corresponding cells in the other quadrants, but its division, as we have seen, is much more unequal than theirs. Examples of this sort might be multiplied indefinitely.

Within certain limits yolk does undoubtedly modify the form of cleavage. No one would dispute, I think, that the meroblastic cleavage of the egg of the teleost or the bird is caused by an accumulation of yolk at the lower pole, and the large size of the macromeres in, *e.g.*, Crepidula is to a certain extent due to the yolk which they contain. But even in these cases size differences, plainly not referable to yolk, appear among the blastomeres, and when we attempt any general survey of the cleavage phenomena the principle wholly fails.

What seems to me the most probable explanation was first advanced by Lillie (No. 21). In a discussion of this subject he says (p. 45): "Unequal cleavage is conditioned by the constitution of the segmenting ovum, and always means the precocious localization of an organ or set of organs in the larger cell." This principle was subsequently elaborated by Conklin (Nos. 5, *a* and 5, *b*), who added the qualification that the size of a blastomere stands in direct relation to the size and the time of formation of the part to which it gives rise, and he explained many of the phenomena in the development of Crepidula by the aid of this principle.

Turning now to equal cleavage, it might be supposed that this form of division was due to a lack of differentiation in the early stages, and, so far as I know, this has been the usual explanation given for it. Rabl (No. 27, *a*) explained the difference between the unequal cleavage of a mollusk and the equal cleavage of an ascidian by supposing that in the former there is a greater differentiation of parts, manifesting itself in size differences among the blastomeres, which does not appear in the latter. In the ascidian this differentiation begins much later, and only then do size differences make their appearance. Rabl believed that an early differentiation was of distinct advantage in the struggle for existence, and that it probably had appeared in the mollusks on that account, while for some reason it was delayed in the ascidian.

From the facts given in the earlier part of this paper, there can be, I think, no doubt that in the embryo of Podarke there is as great a differentiation, appearing as early as in any form with the equal type. The polar differentiation is obviously as well marked. A bilateral arrangement of parts, foreshadowed by the constant relation of the polar furrow to the body axes, is evidently present, and the only doubt would be whether in the 4-cell stage there may not be two possibilities of orientation, one of which the egg chooses before it develops much farther. We might assume that in the later cleavages a differentiation suddenly appears, *e.g.*, at the 64-cell stage, so that from that time on bilateral divisions occur. I know at present of no way by which we could prove or disprove this supposition. From a careful study of the egg, however, I do not believe that such is the case. At the 64-cell stage and later, marked differentiations are evident; but it is to my mind much more reasonable to suppose that a differentiation has been present from the beginning than that it suddenly appears at this stage. I do not mean by this that the material is completely marked off in the unsegmented ovum, but that in Podarke, as in Amphitrite, a gradual differentiation appears as development progresses, and that the process is essentially the same in the two cases.

The important differences to be explained between the cleavage of Podarke and forms with equal cleavage are these: 1. In Amphitrite, Nereis, Arenicola, etc., D is larger than either A, B, or C; in Podarke all four cells are equal. 2. In Amphitrite, etc., the first generation of ectomeres is smaller than the cells below them; in Podarke they are all alike. 3. In Amphitrite, etc., 2d is much larger than either of the other three members of the same quartette; in Podarke they are all of the same size. 4. In Amphitrite, etc., 4d is much larger than 4c, 4b, or 4a; in Podarke again they are of the same size.

I have given above my reasons for assuming that lack of differentiation is not responsible for these size differences, and in two previous articles (Nos. 29, *a* and 29, *b*) I have attempted to explain them by applying the principle of "precocious segregation" proposed by Lillie and modified by Conklin. In other words, I believe that the equal cleavage of Podarke is due to the fact that in the cell D there is accumulated a smaller amount of material destined to produce certain definite parts of the body than in those forms with the unequal type.

From the cell D first arises 2d, which in Amphitrite gives rise to the entire ectoderm of the body behind the first somite, and to a considerable portion of the ectoderm of the head. Essentially the same fate has been described for it in Nereis and Arenicola. In Podarke the cell 2d divides at first very much as in the other forms, but from the first, as was to be expected from its small size, a much smaller amount of the trochophore arises from it than from the corresponding cells in the other genera. In the later stages, when the trochophore is completed and begins to elongate, only a narrow band of ectoderm near the posterior end has arisen from 2d, all of the dorsal ectoderm in front of this having been derived from cells which migrated through the dorsal break in the prototroch (Pl. XL, Fig. 59). Not only in amount, but in rate of development, is 2d in Podarke less than in the other forms. Making all allowances for the slow development due to unfavorable conditions, there is, I think, no doubt that Podarke develops the products of these cells, *viz.*, dorsal ectoderm of the larva and trunk ectoderm, more slowly than does Amphitrite. If study of the pelagic larvae should subsequently prove that this slow development is really due to the unfavorable conditions surrounding the embryos in confinement, the other part of the argument, that only a very small portion of the body is composed of these cells, still retains its force; but the rapid development of the entoderm cells, when compared with Amphitrite, would indicate, I think, that the enfeebling force of environment is really not responsible for the slow development of ectodermal tissue.

Again, 4d is large in unequal, small in equal cleavage. This fact I believe to be correlated with the small amount and slow development of mesoderm derived from 4d in Podarke when compared with other forms. As already described (see p. 431), the germ bands derived from 4d arise very late in the development, and their cells divide slowly, so that at a time when these bands in Amphitrite contain a great many cells there are in Podarke only two on a side. This slow development of mesoderm is also characteristic of Lepidonotus (No. 22). Further, in Podarke the greater part, if not all, of the mesoderm of the trochophore is composed of the larval mesoderm arising from the third quartette of ectomeres; hence the definitive mesoderm appears late in the development, and in accordance with our theory its Anlage in 4d is small when formed. So far, then, our principle holds good for 4d.

We have already seen that the larval mesoderm of Podarke arises asymmetrically, and that 3b does not contribute to its formation. Objection might be made to the above theory on the ground that, if it were true, since 3b does *not* contain larval mesoblast, it should be smaller than 3a, which does. I believe, however, that 3b contributes a larger amount of material to the stomodaeum than does 3a. As described on p. 426, a cell very similar in size to the mesoblast arising from 3a is formed at about the same time as the latter in 3b, and I at first supposed that it contributed to the mesoblast formation. Careful examination, however, failed to show any trace of it in the segmentation cavity, and I believe that its fate is as above described; so that a larger part of the stomodaeum arises from 3b than from 3a.

We have now accounted for the small size of 2d and 4d, and this explanation carries with it the explanation for the equality of D with the other cells in the 4-cell stage. There remains to explain the reason for the equality between micromeres and macromeres in the 8-cell stage. This may be due in some meassure to the small amount of yolk, but the comparatively large size of the micromeres is, I believe, correlated with the unusually large development of the umbrella as compared with the subumbrella of the trochophore, and with the fact that a large portion of subumbrellar ectoderm really comes from the first quartette of micromeres. (See p. 413.) In discussing this point in a previous paper (No. 29, *b*) I overlooked the fact that the prototroch cells of Amphitrite are relatively much larger than those of Podarke, and I argued that the relatively larger cross cells in the latter would account for the relatively larger size of the first group of micromeres. The larger size of the prototroch cells in Amphitrite would probably compensate for the small cross, and so the argument loses its force; but the further consideration, that a very large part of the subumbrellar ectoderm in Podarke arises from these cells, is in itself a sufficient explanation for their size. We have already seen that the amount of ectoderm arising from these migrating cells in Amphitrite is comparatively very small.

Among the mollusks, I believe that the evidence at our disposal sustains the theory. In Crepidula the peculiarities of the 8-cell stage are probably to be explained by the presence of abundant yolk in the macromeres, but the fact that D is no larger than A, B, or C is due to the slow development of the characteristic products of that cell — the shell gland and the mesoblast. In Unio the principle certainly applies. Unfortunately, we know too little about the later larval stages of other mollusks, whose cell lineage has been studied, to draw any very positive conclusions. In Umbrella (No. 14), D is smaller than A, B, or C. Heymons did not follow the history of the descendants of this cell very carefully, but describes the shell gland as arising very late. If analogy can be depended upon at all, this gland arises from 2d and our theory holds.

The application of this principle to later stages demonstrates, as I believe, its correctness. To mention but a single example: Perhaps the most noticeable feature of the development of the cross in Podarke is the way the anterior arms divide up into very small cells, while the cells of the posterior ones remain large. This is, I believe, correlated with the development of the large, thin-walled dorsal ectoderm, while the ventral ectoderm of the umbrella is much thicker and gives rise to the eyespots and the frontal (excretory?) bodies, the former having a very much greater superficial extent than the latter. It is probable also that some cells of the latter are thrown off and absorbed.

Equal cleavage, then, is not, I believe, the expression of a lack of differentiation in the ovum and early embryo, but is due to the fact that a certain amount of formative material, which in other genera is sufficient, when accumulated in a single cell, to increase noticeably the size of that cell, is here present in so small a quantity that no size differences appear. This small amount of formative material is correlated either with the small size of the organ to which it gives rise, or with the late development of that organ.

Mesoblast and Larval Mesoblast.

As already stated in the descriptive portion of this paper, a double origin of mesoblast seems to occur in a number of annelids and mollusks, the phenomenon apparently being more widespread in the latter than in the former group. To the one tissue Lillie gave the name "larval mesoblast," because of its purely larval function. The cells composing it early lose their connection with one another, and wander through the segmentation cavity, where they become elongated and form the larval muscles. The term "mesenchyme" has been so generally applied to cells having this structure and position that Lillie uses the name here and supposes that these cells are phylogenetically related to the mesenchyne cells of ancestral forms which originally arose from ectoblast, but in this case are massed into a single cell.

The second source of mesoblast in Unio is at the posterior end of the body, arising from the cell 4d, and differs from the first in that its cells are grouped into definite germ bands, and give rise to the mesoderm of the adult body.

As we have already seen, while the definitive mesoblast of annelids and mollusks usually arises as in Unio from the cell 4d, an additional *larval* mesoblast having a different origin but similar function in each case has been described for Physa, Planorbis, and Crepidula, among the mollusks, and for Aricia and Podarke among the annelids. Conklin (No. 5, *a*, p. 151) has stated his belief that the larval or primary mesoblast is phylogenetically the older, and indicates a primitive radial origin for this layer, while it has been replaced in the ontogeny by the secondary or bilateral mesoblast, arising from 4d.

Professor Wilson, as a result of renewed investigation on platodes[1] (see p. 462), has eliminated some apparent inconsistencies between these forms and the annelids, lamellibranchs, and gasteropods, and has shown that Lang was probably correct in his derivation of the mesoderm in polyclades from the second and third quartettes of micromeres. In an exceedingly interesting and suggestive article Professor Wilson has proposed the theory that this larval mesoblast (or, as he calls it, "ectomesoblast," because of its origin from ectoderm) is a distinct tissue from the definitive "entomesoblast" (so called because it arises from entoderm), and is homologous with the mesenchyme of the turbellarian ancestors of the annelids, while the mesoderm from which the adult structures arise is phylogenetically younger and is represented prophetically in the ontogeny of such a form as Discocoelis by the peculiar bilateral division of the cell 4d. The ectomesoblast and entomesoblast are therefore phylogenetically of different origin, a point previously urged by Meyer (No. 23).

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[1] See also Appendix to Literature.

Professor Wilson has certainly made out an attractive theory, and the history of the two sorts of mesoderm in Podarke, especially the long-continued connection of the mesoblast with the entoderm, at first sight lends confirmation to his view. For reasons given below, however, I am not inclined to accept it as stated, and propose instead a suggestion which seems to me more in accordance with the facts.

I believe that no hard-and-fast distinction can be made between the two kinds of mesoblast. This belief is based on the following facts:

In Nereis, Wilson (No. 34, *d*) has shown that cells from the anterior ends of the germ bands early separate from the bands and pass forward into the segmentation cavity, where they give rise to the larval musculature, which corresponds exactly in structure and function with the larval mesoblast of Unio or Podarke.

In Lumbricus, also, Wilson (No. 34, *a*) has shown that previous writers were in error in supposing an origin of mesenchyme distinct from mesoderm, and that the mesenchyme of the embryo is really formed from the anterior cells of the germ bands which have migrated forward and taken on a mesenchyme structure. Similar observations have been recorded by Hatschek (No. 11) and Von Drasche (No. 7). (See, however, p. 428.)

To these observations must be added those of Wilson on Hydroides (No. 34, *b*): "In its earliest recognizable condition the mesoblast band consists of a group of three or four cells, wedged into the angle between the posterior part of the archenteron and the ectoblast. Beside this, there are a number of scattered cells lying in the narrow cleavage space. The mesenchyme cells appear to graduate both in form and position into those of the germ bands. The latter appear about the time of gastrulation as two bilateral masses of cells that are pushed into the cleavage cavity near the blastopore. Some of these appear to pass forward and give rise to the mesenchyme; the remainder form the secondary mesoblast bands." Here again we have a larval mesenchyme which apparently arises from the anterior ends of the germ bands, and its cells must be homologous with those of the definitive bands.

In the most recent paper on annelid cytogeny, Eisig (No. 8) has described a very different origin of mesoblast from what is found in any other annelid. Instead of arising from 4d, the definitive mesoblast (coelomesoblast) arises from 3c and 3d (it would therefore be "ectomesoblast" in Wilson's sense), while the larval (paedomesoblast) arises from 4d, and not from the portion of 4d which in Nereis or Podarke gives rise to mesoblast, but from the portion which in those forms becomes a part of the entoderm wall.

Capitella, from the large proportion of abnormal eggs found in the tubes, seems to have been an especially unfavorable form for the study of cytogeny. It is difficult to believe that one of Professor Eisig's scientific attainments could have committed so serious an error, but these results are so very different from anything else that has been described, that even though bearing in mind Eisig's strictures on "Die Thatsachen nicht achtenden Verallgemeinerungen," one may be pardoned, for the present at least, doubt whether normal specimens were studied. To these differences, which are mainly of importance in a discussion of cell homology, I shall return later (see p. 464). Of importance in this connection is the fact that, according to Eisig, the two sorts of mesoderm are not absolutely distinct, but that cells may migrate out from the "Coelomesoblast" and become "Paedomesoblast." Eisig believes that the two kinds of tissue may have originally come from a common Anlage. Eisig further argues that neither can properly be said to arise from ectoderm nor entoderm, but rather from cleavage cells, inasmuch as at the time of formation there has been no differentiation into germ layers, and he accepts Meyer's theory that the mesoblast bands represent a gonad tissue, from which may arise by differentiation all the mesoderm of the body, including new germ cells.

From these facts it seems to me, if we accept Professor Wilson's theory, we are bound to believe in two non-homologous sets of larval mesenchyme; the one arising from ectoderm, found, for example, in Podarke, and the other arising from the anterior ends of the germ bands and found in Nereis and Lumbricus. These two sets apparently do not, as a rule, exist together, only one case, that of Capitella, having been described. On the other hand, no one has proved, so far as I know, that no "mesenchyme" arises from the germ bands in cases where a larval mesenchyme exists. Either, then, we must assume two sets of non-homologous organs having exactly the same structure and function, and in at least one case existing side by side, or (and this seems to me the more reasonable assumption) we must regard both mesenchyme and mesoderm as morphologically the same tissue, apparent differences in their mode of origin being of no significance. If, as I believe, the trochophore represents an ancestral stage in the phylogeny of the annelids, the mesodermal structures found in it undoubtedly represent the mesoderm of the ancestral form. Whether the origin of metamerism was due to a process of budding, or to growth and subsequent metamerization, is not essential for the present discussion. In either case, as Wilson has pointed out (No. 34, *c*) (it is only fair to say that the fact was used as an argument against the ancestral significance of the trochophore), the trochophore at the present time is more than a mere ancestral stage, for it contains in a concentrated form the Anlage of the whole future body. Mead has proved that in Amphitrite all the ectoderm for the body behind the first septum arises from a group of cells which surround the proctodaeum of the young trochophore and are descended from a single cell, the first somatoblast, and probably the same thing occurs in Podarke. The grouping of the mesoderm at the posterior end of the body is also a familiar feature of annelid ontogeny.

Now, as there is no need to assume a phylogenetically new formation of ectoderm for the body as distinct from the head, so I see no need for assuming a new formation of mesoderm. This is evident in Nereis or Lumbricus, and I see no reason why a difference should be made in the case of Aricia or Podarke. In the former case there has simply been a more complete concentration of mesoderm than in the latter. If the facts bear on the point at all, they tend to show an origin of mesoderm from ectoderm rather than from entoderm, though this concentration of material must have led to such changes that we are hardly justified, from the present position of the mesoderm, in drawing any conclusions as to its primary mode of origin.

I believe, therefore, that the mesoderm cells collected at the posterior end of the trochophore larva, and which we know as the definitive mesoblast, represent neither entodermal evaginations nor gonad tissue, but that they represent the mesoderm of the body, which is morphologically continuous with that of the head (as we know it is in Nereis or Lumbricus), and which has been concentrated at this point to provide for the needs of the elongating body. In some cases this concentration is less complete than in others, so that some forms seem to have a double origin of mesoblast, but this (apparent) double origin in no way interferes with the morphological unity of the tissue. Whether the mesoderm arose originally from ectoderm or from entoderm or from neither, we are not at present in a position to say.

Rabl's theory of the mesoderm (No. 27, *c*) seems to have rested too much on an error of observation (Hatschek's description of the mesoblastic teloblasts in Amphioxus; see also Minot's criticism, No. 24, p. 155), and the "Coelomtheorie" of the Hertwigs (No. 13) makes, as I believe, too sharp a distinction between mesoderm and mesenchyme. In the introduction to his paper on Nereis, Wilson hopes, by a study of cytogeny, to break away from the deadlock of opinion concerning the mesoderm, but as I understand his conclusions on p. 393, he secured no evidence bearing on the primitive mode of origin of this layer. In his later paper (No. 34, *g*) Professor Wilson has suggested, as above stated, that the definitive mesoblast came from entoderm, while the secondary is of ectoblastic origin. The conclusion follows that the mesoblast of the turbellarian is not homologous with the definitive mesoblast of higher forms, but only with the larval.

If we once assume that the mesoderm in different groups must have exactly the same cellular origin in order to be homologous, we land ourselves in an inextricable maze of difficulties. Especially is this true if, in addition to the strictly embryological data, we take into consideration the facts of regeneration and bud development. The literature of this subject is too familiar to need citing. (See, however, Nos. 34, *e*, and 18.) Eisig (No. 8) devotes a considerable amount of space to this question, and since any general review of the various theories would be largely a repetition of what he has said, I shall not attempt it here. Meyer (No. 23) had previously maintained that the definitive mesoderm represents gonad tissue, while the mesenchyme had a different origin. Eisig accepts this position not only for the first-named tissue, but extends it so as to include the mesenchyme as well, and supposes that both sets of mesoderm are really gonad cells which may be mixed with any other cells without losing their characteristic qualities or affecting the character of the latter. From these may arise all the other cells of the body, though in the actual ontogeny of the individual the outer and inner layers having been provided for already, they develop only into the middle layer.

As said above, the accumulation of mesoblast at the posterior end of the body seems to me a secondary condition, connected with the need of supplying material for the elongating embryo, and I see no evidence that it has now, or ever has had, a gonad structure. The changes which must have occurred since the layer was first differentiated are so great that it does not seem to me we are justified in claiming positively any especial mode of origin for it.

We must, I think, go back to the position taken originally by Wilson (No. 34, *e*), and which, I judge, he has subsequently abandoned, that, "We must primarily take anatomy as the key to embryology and not the reverse. Comparative anatomy, and not comparative embryology, is the primary standard for the study of homologies." The mesoblast of the mollusk or the annelid is a single continuous structure, not a mixture of non-homologous structures, and the mesoblast of the platode is homologous, in the proper use of the word "homology," with the whole and not with a part of it. Whether this conclusion would apply to more widely separated groups might perhaps be doubted, for the mesoderm apparently has very diverse modes of origin (see Montgomery, No. 25), but in forms as closely related as the annelids, mollusks, and platodes I believe that it is correct; and, as said before, coenogenetic modifications must have been so great that we are hardly at liberty to assume that the diverse modes of origin are proofs of the non-homology of this layer in other cases.

Cell and Regional Homologies.

One of the most important problems connected with the study of cell lineage, especially in its bearing on the meaning of cleavage, is the question of cell homology. The wonderful agreements which exist between the cleavage stages of annelids, lamellibranchs, gasteropods, and platodes, when viewed in the light of widely accepted homologies between the larvae and adults of these groups, have led most workers to propose for cleavage stages an homology as complete and accurate as for the adult organs. And, indeed, if a blastomere of an early cleavage stage in a gasteropod is identical in position and origin with a blastomere in an annelid, and the descendants of each give rise to an organ which can be considered homologous in the two cases, the cell homology would certainly be proved. As Conklin has said, "I believe there is no escape from the conclusion that the protoblasts of homologous organs are as certainly homologous as are the organs to which they give rise; that the protoblasts of homologous layers are as surely homologous as are these layers, and that the protoblasts of homologous regions are as much homologous as are those regions"; and, "We therefore reach the conclusion that, in related organisms with determinate cleavage, homologies may be predicted of single cells, whether they be protoblasts of the nervous system, the excretory system, or the locomotor apparatus; of the ectoderm, the mesoderm, or the entoderm; of the right or left, the anterior or posterior portion of the body."

If this be true, cleavage similarities have as great a phylogenetic value as larval or adult similarities, but I shall try to show that the number and completeness of these resemblances have been greatly overestimated; and that the second of the above propositions by no means follows from the facts at our disposal.

The first suggestion I have been able to find along this line is that of Rabl (No. 27, *a*): "Ueberhaupt scheint es nach allen bisherigen Beobachtungen nicht unwahrscheinlich zu sein, dass jede mehr oder weniger scharf umschriebene Thiergruppe ein gemeinsames für alle Glieder dieser Gruppe giltiges Furchungs-Schema besitze, und dass es daher durchaus nicht undenkbar sei, dass man künftig einmal aus der grösseren oder geringeren Uebereinstimmung im Furchungsprozesse auf eine engere oder weitere Verwandtschaft zweier oder mehrerer Thierformen werde schliessen können." Inasmuch, however, as Lillie (No. 21) has shown that many of Rabl's observations were incorrect, this hypothesis must be considered as a more or less fortunate guess than as following logically from his results.

At the time when Professor Wilson's work on Nereis appeared, practically the only papers available for comparison were those of Lang on Discocoelis (No. 19), Blochmann on Neritina (No. 3), Whitman on Clepsine (Nos. 33, *a* and *b*), and von Wistinghausen on Nereis (No. 35). In addition, Wilson referred to the then unpublished observations of Conklin on Crepidula. While the polyclade agreed with the annelid and mollusk in the most remarkable fashion in the details of its cleavage, it differed very decidedly in at least one important particular, *viz.*, the origin of the mesoblast.

These differences and the conclusions Wilson draws from them are as follows : "The general later history of the blastomeres thus formed is as follows : In the polyclade the first group of micromeres gives rise to the entire ectoblast, the second and third groups to the mesoblast, the macromeres to the entoblast. In the mollusk and annelid, on the other hand, the second and third groups of micromeres give rise to ectoblast, like the first set, and the mesoblast arises subsequently. This remarkable divergence between the polyclade on the one hand and the mollusk and annelid on the other is a fact of capital importance, for it proves that cells having precisely the same origin in the cleavage, occupying the same position in the embryo, and placed under the same mechanical conditions, may nevertheless differ fundamentally in morphological significance."

Extending the comparison in the mollusks, Wilson describes the peculiar cross figured by Blochmann in Neritina, and compares it with the similar structure found in Nereis. Making all due allowances for Blochmann's error, which Conklin had corrected, he finds that the two structures are composed of cells of a very different generation, and occupy a very different position with reference to the axis of the body, in the annelid, from what they do in the mollusk. Wilson's conclusion is that these structures are analogous and not homologous, and their origin is in some way connected with mechanical conditions of cleavage.

Lastly, Wilson shows that the velum of the mollusk and the prototroch of the annelid have a very different cell origin, but is careful to insist that this fact does not, in his mind, invalidate the idea of an homology between the completed organs.

Wilson decides, at the end of his discussion, that it is necessary to be very cautious about drawing morphological conclusions from the comparative study of early cleavage stages. Blastomeres having precisely the same mode of origin and precisely the same spatial relations to the rest of the embryo are by no means necessarily equivalent, either physiologically or morphologically, and the early cleavage stages in themselves have little morphological value. The respective value of the blastomeres must be determined by their ultimate fate, and this is an indispensable datum for the study of comparative embryonic anatomy. *The fundamental forms of cleavage are primarily due to mechanical conditions, and are only significant morphologically in so far as they have been secondarily remodelled by processes of precocious segregation.* (The italics are in the original.) Since, however, the facts seemed to him to show that this process has taken place to a greater or less extent, Wilson closes his paper with a plea for the study of cell lineage as the best means by which we may hope to obtain a firm basis for a comparison of the germ layers.

In his paper on Unio (No. 21), written two years later, Lillie, while recognizing the fact that difficulties exist in the way of the assumption, argues for an homology of cells, basing this argument on the origin of the mesoblast from a corresponding cell in a wide range of annelids and mollusks, and on the similar origin and fate of three quartettes of ectomeres in all these forms. Lillie thus argues for a cell homology. His definition of this term, as I understand it, is that two cells whose products are homologous must be themselves homologous, even though they have a different origin in the cleavage. Lillie calls attention to one important difference between Nereis and Unio, *viz.*, that a cell which in Nereis is a stomatoblast, in Unio gives rise to the larval mesoblast. His explanation of this difference is that the form of cleavage being constant, whenever a new organ appears, it must appear in some cell already present, the formation of a new cell being an impossibility. Hence this larval mesoblast, being an ectodermal structure, must make use of a cell which in other cases remains in the outer germ layer.

In his lecture on "The Embryological Criterion of Homology" (No. 34, *e*), Wilson, while recognizing the "marvelous agreements" in the cytogeny of related forms, argues that as we extend the comparison "the contradictions reach a climax." The facts of regeneration, also, show important differences from embryological processes, differences which seem to invalidate the whole germ-layer theory. The conclusion which Wilson reached was that, for the study of homologies, adult structures are of much more value than embryological, since homologous adult parts may arise from non-homologous Anlagen ; and, conversely, cleavage cells having the same origin give rise to non-homologous organs. While most of his lecture deals with embryonic structures which appear after the cleavage, it is, I think, evident that Professor Wilson intended to discredit the study of cytogeny as a means of determining homologies.

Mead (No. 22) devoted considerable space to a discussion of this question of cell homology, which he defined as follows : "Essential similarity in origin and fate will be considered a sufficient criterion of the homology of cells, as it is, by common consent, of tissues and organs." Mead first shows that in general the mode of origin and the fate of the quartettes of ectomeres are the same in all annelids and mollusks. Then, examining the cleavage more in detail, he finds that in Amphitrite and Clymenella the primary and secondary trochoblasts are cell for cell the same ; and, further, in Scolecolepis, which has a suppressed trochophore, these very cells are diminutive, as might be expected from a non-functional organ. This prototroch formation is very different from the process as described for Nereis, but Mead gives reasons for believing that Wilson's description was erroneous.

Mead further shows that the objection raised by Lillie to cell homology because of the varying fate of cell $3a_{2.2}$ is not valid, because in neither case was the whole of this cell involved. In both cases it divides horizontally, and while the lower portion in Nereis becomes stomatoblast, in Unio it is the upper portion which becomes larval mesoblast.

Another case of cell homology is the apical rosette, which probably has exactly the same origin and fate in all the annelids studied, and in Crepidula among the mollusks. The slime glands of Amphitrite also are homologous in position, and probably in fate, with the "head kidneys" of Nereis.

The fate of the remaining cells of the upper hemisphere was, according to Mead, so uncertain that he did not attempt to follow homologies, and the same was true of the lower hemisphere, except, in a general way, the somatoblast 2d, and, more especially, one of its descendants, the small cell, $X_{1.2}$, which apparently has the same origin and fate in Nereis, Amphitrite, Unio, and Clymenella.

The most complete homology, according to Mead, is shown in the origin of the mesoderm. This always arises leiotropically at the ideal 64-cell stage, and is one of the fourth generation of micromeres given off from the cell D. A serious discrepancy here and a strong argument against cell homology was the origin of the mesoblast in Discocoelis, where, according to Lang (No. 19), although the general form of the cleavage is the same as the annelid, the mesoderm arises not from 4d, but from the second and third group of micromeres, the cell 4d forming a part of the entoderm. Lang's figures, however, show a bilateral division of 4d very different from the division of the other members of this quartette, and Mead has suggested that possibly there was an error in the interpretation, and that mesoblast may arise from this cell in the platode as well as in the annelid.

In his "Embryology of Crepidula," published a little earlier than Mead's paper, and in a subsequent lecture (No. 5, *a* and *b*), Conklin has extended the comparison between annelids and mollusks still farther. After mentioning the similarities above noted, he says: "To this list of resemblances between the annelid and the mollusk, which I can confirm in the case of the gasteropod, I have been able to add the following: The rosette series of the gasteropod is exactly like the cross of the annelid in origin, position, and probably in destiny. The intermediate girdle cells of the annelid are like the cross of the gasteropod in origin, position, and destiny (at least in part). The differences, therefore, between the annelidan and molluscan cross which Wilson emphasizes are not real ones. The trochoblasts of the annelids and gasteropods are precisely similar in origin and destiny, *at least in part.*" (The italics are mine. See p. 466.) "In some annelids (Amphitrite, Clymenella, Arenicola) the prototroch is completed by cells of the same origin as in Crepidula and Neritina. The differences which Wilson points out between these two structures do not therefore exist. In both annelids and mollusks the prototroch lies at the boundary between the first quartette on one side and the second and third on the other. In both there is found a preoral, adoral, and a postoral band of cilia. In the gasteropod the apical cells give rise to an apical sense organ, such as is found in many annelid trochophores. The supraoesophageal ganglia and commissure apparently arise from the same group of cells in annelids and gasteropods. The fourth quartette in annelids and gasteropods contains mesoblast in quadrant D, but is purely entoblastic in quadrants A, B, and C. A fifth quartette is formed in gasteropods and some annelids (Amphitrite) and consists of entoblast only. In the gasteropod, larval mesoblast arises from the same group of ectoblast cells as in Unio, differing, however, in this regard, that it is found in quadrants A, B, and C, whereas in Unio it is found in quadrant A only. To this list of accurate resemblances in the cleavage cells may be added the fact that among annelids and mollusks the axial relations of all the blastomeres (except possibly the four macromeres) are the same.

"The cause of such resemblances, like the cause of determinate cleavage and of the constancy of specific characters, must be found in protoplasmic structure, and I cannot escape the conviction that these likenesses belong to the same category with the fundamental resemblances between gastrulae, larvae, and adults. Whatever criterion of homology one may adopt, — whether similarity of origin, position, history, or destiny, or all of these combined, — certain of these resemblances in cleavage bear all the marks of true homologies."

The polyclade cleavage offered difficulties which were great, "perhaps irreconcilable," but Conklin argues that, since we find no perfect homology between adult structures, we need not expect to find perfect homology between cleavage stages. Professor Conklin's conclusions may, I think, be fairly given in the following passage (No. 5, *a*, p. 198): "If organs which are homologous among annelids and mollusks, such as the prototroch, the apical sense organ, the stomodaeum, and the ventral plate, can be traced back in their development to certain individual cells of similar origin, position, size, and history, are not these cells truly homologous? If not, where in this developmental process shall we say that homologies begin?"

Conklin further distinguishes between cell and regional homology, the latter appearing, for example, between annelids and gasteropods on the one hand, and the ctenophores on the other. Further, if I understand him correctly, although he gives no formal definition, he would distinguish between complete and incomplete cell homology. I am able to see very little distinction to be logically made between an incomplete and a regional homology, and it seems to me a clearer definition of cell homology is to be desired. If cell homology is the resemblance which exists between two organs whose Anlagen are merely *similar* and not *identical* in origin, I have no objection to the use of the term in recent writings; but it seems to me very little distinction can be made between this and regional homology, and I see no reason why, using this definition, all homologies are not cell homologies. The phrase "incomplete cell homology" is to me a contradiction of terms.

I have no desire to split hairs over a mere definition, and it may be that the term is convenient and should be retained (for example, to designate an homology between two organs, not determined by adult structure alone, but by a similarity in cellular origin as well). At the same time it seems to me desirable to emphasize the distinction between the complete and the incomplete, as the hasty reader of many recent cell-lineage papers would, I think, be in danger of carrying away too exaggerated a notion of the number and importance of the former. To this point I shall return.

Wilson, in a paper already quoted, has reinvestigated the platode cleavage, and has shown that although the cleavage in its general character agrees perfectly with the annelid and gasteropod, yet the mesoblast, precisely as described by Lang for Discocoelis, arises from the second and possibly, to a limited extent, from the third, quartette of ectomeres. While this breaks down Mead's criticism of Lang, it at first sight seems to revive the old difficulty in the way of accepting homologies between the two groups. In view of the recent discovery of larval mesoblast in annelids, gasteropods, and lamellibranchs, however, Wilson believes that the apparent contradiction is in reality new proof of the homology as showing an homology between the *larval mesoblast* of the annelid and mollusk, and the *adult mesenchyme* of the platode. (See the section on the mesoderm, p. 449.)

Another difficulty in the way of cell homology has been the cleavage of Polychoerus, which, according to Gardiner (No. 9), is of the bilateral type. With the aid of Leptoplana and Discocoelis for comparison, Wilson[1] has reëxamined Polychoerus, and finds that it has the true spiral type of division and is thus brought into line with the other genera.

In the light of these facts Wilson has abandoned the position taken in his lecture and has gone back to that of his first paper on Nereis, though his views are even more extreme than in 1892. His conclusions may be summarized in the following extracts (No. 34, *g*): "The phenomena shown in the history of the micromere quartette in annelids, platodes, and mollusks render it highly probable, if they do not actually demonstrate, that development may exhibit ancestral reminiscence as clearly in the cleavage of the ovum as in the later formation of tissues and organs. These facts may well give us hope that when the comparative study of cell lineage has been carried farther, the study of the cleavage stages may prove as valuable a means for the investigation of homologies and of animal relationships as that of the embryonic and larval stages.

"These facts seem on the whole to emphasize the importance of cell formation in development, and it would be difficult to explain ancestral reminiscence [*e.g.*, the small "enteroblasts" of Aricia, which he regards as ancestral rudiments, and the larval mesenchyme of Unio or Crepidula] in cell lineage under any view which does not recognize in cell outlines the definite boundaries of differentiation areas in the developing embryo."

Eisig's study of Capitella cleavage brings to light many similarities with the cleavage of other annelids, especially with Nereis (No. 34, *d*), which he used most frequently for comparison, and he finds that in general the cleavages are remarkably alike in the two cases; so that "Die Parallele, welche

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[1] I am indebted to Professor Wilson's courtesy for permission to quote this, as yet unpublished, observation.

Conklin mit Recht als wunderbar bezeichnet, wird nun aber durch mehrere Nachweise dieser meiner Arbeit noch erheblich gesteigert."

The origin of the mesoderm from a cell of the third quartette is not an argument against this position, because the mesoderm cells are not differentiated but are undifferentiated cleavage cells, corresponding with germ cells of the lower animals, and may be mixed with (beigemengt) various cleavage cells without affecting the inherent quality of the latter. That the mesoderm is mixed with a macromere, or a micromere, is shown by the fact that the whole micromere or macromere never passes into the mesoderm, but rather buds off a daughter-cell from which the mesoderm arises. Inasmuch as this mixing does not affect the character of the mother-cell, its homology with other cells in other groups which do not happen to contain mesoderm is not affected.

I may remark, in passing, that this conception of the wandering character of the mesoderm cells would, if accepted, remove one of the strongest arguments for cell homology. The constant position of the mesoblast pole cells and their origin from 4d have been the strongest argument in support of the theory.

Lastly, in a short preliminary, Child (No. 4) has taken a definite stand against cell homology, basing his claim on the absence of a prototroch in Sternaspis, — where, however, it seems to me, his criterion of homology is too severe, — and on a comparison of the paratroch of Arenicola with that of Amphitrite, the origin being very different in the two cases. It is only fair to say, however, that the origin of the prototroch is the same in both.

The development of Podarke not only has furnished no new evidence for complete cell homology, but, on the contrary, shows that many which have been assumed by previous writers are not of wide application. A comparison of the various details will be instructive.

1. *The Apical Rosette.* — The cells composing this have the same origin, and probably have the same fate, in a number of different annelids and mollusks. The apical tuft of cilia is, in

many cases at least, carried by them. Whether they divide to form eight cells, or remain four in number, does not affect the homology, which in this case is probably complete.

The other cells of the upper hemisphere have undoubtedly the same general fate, but no comparison can with our present knowledge be made between them. The mucous glands in Amphitrite have the same cell origin as the large glands in Nereis, but the comparison does not extend farther. If we believe in ancestral rudiments in cleavage, we may maintain that the small cell on each dorsal arm of Podarke, which corresponds in position to this gland, is really a rudiment of it become functionlesss in the latter genus. It certainly does not give rise to a gland, but I believe that it afterwards enlarges and enters into the general ectoderm of the head. The cross cells differ from their first formation in the number and arrangement of cells, so that no comparison can be instituted.

2. *The Trochoblasts.* — Mead[1] has considered the precise similarity between the formation of these cells in Amphitrite and Clymenella, the similarity extending not only to the primary but to the secondary trochoblasts. In Arenicola, also, the prototroch is formed as in Amphitrite, and thus far the homology holds. As stated above, however, the Podarke prototroch arises in a different way. The comparison can best be seen from the table.

	Primary Trochoblasts.		Secondary Trochoblasts.	
Amphitrite Arenicola Clymenella	$1a_{2.1.1}$ $1a_{2.1.2}$ $1a_{2.2.1}$ $1a_{2.2.2}$	etc., in all four quadrants.	$2a_{1.1.1}$ $2a_{1.1.2}$ $2a_{1.2.1}$	in A, B, and C quadrants.
Podarke.	The same as the others.		$1a_{1.2.2.2}$ $2a_{1.1.2}$ $2a_{1.2.1}$	in A, B, and C quadrants.

In the description of the trochoblasts, I have distinguished between "tertiary" and "secondary." For convenience both are here grouped under "secondary."

Thus, in Podarke, three out of the twenty-five cells which make up the completed prototroch are different from those found in the other cases mentioned. This difference is slight, but enough to disprove a complete homology.

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[1] See Appendix to Literature.

In Nereis, according to Wilson, while the cells corresponding to the primary trochoblasts of the other genera appear in each quadrant, the upper sinistral one is pushed out of the prototroch ring, and the completed organ is composed of only twelve cells. The origin of the secondary trochoblasts was not determined.

Mead has thrown doubt on the accuracy of these observations and a reinvestigation of the subject is perhaps to be desired. I can discover no internal evidence of their incorrectness. If true, they strengthen the position here taken and show a lack of complete cell homology between the prototroch of Nereis and the other annelids.

Conklin also has argued for a very complete homology between the trochoblasts of Crepidula and those of annelids, but a comparison of his description of the velum of Crepidula with the annelid prototroch seems to me not to bear out the precise similarity which he maintains. There are in Crepidula four cells corresponding in origin to the four primary prototroch cells of Annelida. Of these, *two* — those of the ventral surface (quadrants A and B) — enter into the formation of the velum, ***but the posterior ones do not,*** unless the whole head vesicle is a part of the velum, for they lie in front of the functionless posterior branch of the velum, which Conklin considers the homologue of the velum in other mollusks and the prototroch of annelids, and behind the functional anterior branch which he considers a new formation. The velum is completed in the ventral portion at least by cells which have the same origin as the secondary trochoblasts of Amphitrite, but proportionally more cells from the second quartette come in, and it is not impossible (p. 134) that some of the third quartette cells may also form a part of the prototroch. The organ occupies a corresponding position in annelids and in mollusks, and I have no doubt that it is homologous in the two cases. The close correspondence in the mode of origin is additional evidence for this homology, but the point I wish to emphasize here is that this homology is not a complete homology, nor does it seem to me as close as Professor Conklin would maintain, nor as close as one would infer from his statement (p. 194, etc.).

3. *The X-Cells.* — In the lower hemisphere the cell 2d has been cited as an example of cell homology, for from it arise the ectoderm of the trunk, the ventral plate, and the growing point. Within the limits of the cell the most important larval organ is the paratroch. The cell origin of this is known only in Amphitrite and in Arenicola, but it is not the same in the two cases. In Podarke, as already stated, I have been unable to find any paratroch, and the comparisons which I have made between the divisions of X in Podarke and those in the other two annelids show absolutely no similarities.

A further point in the development of Podarke is the relatively small amount of dorsal ectoderm arising from 2d. As shown in Pl. XL, Fig. 59, this forms only a comparatively narrow band around the proctodaeum, all the rest of the dorsal ectoderm having arisen from cells which migrated through the dorsal break in the prototroch. Either, then, we must assume that 2d is not completely homologous in Podarke and in Amphitrite, or we must assume that the portion of the trochophore lying just behind the prototroch is not homologous in the two cases. Of the two, the former seems the more reasonable.

The small cell, $X_{1.2}$, arises in the same manner and occupies the same position in all the forms studied. Its fate is unknown, except for the general statement that it forms a part of the proctodaeal wall. The constant position of this small cell must have some meaning, although I am not able at present to say what that is. It may be another case of complete homology, and for the sake of the argument we may assume that it is, though it should be remembered this has not been proved.

4. *The Mesoblast.* — There remains one more cell for which a complete homology is assumed in the various forms, and that is the cell 4d, which, with but one exception, contains the definitive mesoblast.

This cell arises from the posterior macromere D, and, so far as its origin is concerned, is alike in all cases. That it is qualitatively different is shown, I think, by the most recent investigations. The following table is not intended to be a complete list of papers where the origin of this cell has been described, but contains the most recent.

	4d contains
Nereis . . .	Mesoderm and a little entoderm.
Aricia	“ “ “
Polymnia . . .	“ only (?).
Amphitrite . . .	“ only.[1]
Arenicola . . .	“ “
Unio	“ and “secondary mesoderm” (entoderm ?).
Umbrella . . .	“ “ “
Planorbis . . .	“ “ “
Crepidula . . .	“ and a comparatively large amount of entoderm.
Podarke . . .	“ and a little entoderm.
Capitella . .	Larval mesoderm and ventral ectoderm.

Here, leaving out of consideration, for the moment, the case of Capitella, we must assume either that the cell 4d is not completely homologous in Podarke and in Amphitrite or in Unio and Crepidula, or we must assume that the mesoblast of the one form is partly homologous with the entoderm of the other ; and here again my preference is for the former assumption. If Capitella be as described by Eisig, and we claim cell homology for 4d, we are driven to the assumption that the mesoblast of Nereis is homologous with the ventral plate of Capitella, and the larval mesoblast of Capitella is homologous with the entodermal portion of 4d in Nereis ; while the definitive mesoblast of Capitella is homologous merely with the larval mesoblast of other forms. As already stated on p. 451, I can hardly believe that these were normal cleavages. If normal, they put an end to all questions of cell homologies, complete or incomplete.

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[1] Professor Wilson has shown that it is not impossible that small cells budded off from the primary mesoblasts in Amphitrite, Unio, Umbrella, Planorbis, and Physa are really entoblasts and not mesoblasts. In Amphitrite, however, these cells do not arise in the same position as in Aricia or Nereis, and they remain at the anterior end of the mesoderm band ; their fate is therefore very different in the two cases. Heymons is positive that in Umbrella these cells are mesoblast, and in Planorbis they lie “in the cleavage cavity” (No. 15, *a*), hence have the proper position at least for mesoderm. In a personal communication (1899) Dr. Holmes assures me that there is no doubt of the mesoblastic fate of these cells. For these reasons I have thought best to regard all these cells as mesoderm until further study shall show that they are not. In Clymenella, also cited by Professor Wilson, we have no evidence that the cells in question do not become mesoderm, and the first division of the primary mesoblasts, as described by Mead, may separate off an entodermal portion or it may be the first division toward the formation of the mesoderm bands. At present we are unable to say which view is correct, and the observations are of little use in this discussion.

The larval mesoblast is an organ whose exact origin is known in a number of groups. It may arise from the second quartette (Unio and Crepidula), from the third (Podarke, Physa, Planorbis), or, *if Eisig be correct*, from the fourth (Capitella). Its exact origin is probably not the same in any two of these cases. It may arise asymmetrically, later becoming symmetrical (Unio and Podarke), or it may be symmetrical from the beginning (Crepidula and Planorbis). Evidently no complete cell homology can be demonstrated here, and we are given two alternatives : either this larval mesoblast is not homologous in all cases, or it arises from cells which are not completely homologous. I prefer the latter assumption.

Other organs of the embryo are the proctodaeum, stomodaeum, and supraoesophageal ganglia. While these are undoubtedly homologous organs, their precise cell origin is different in the different cases.

I have described these facts at some length, because it seemed to me that the more we investigate the subject the more difficulties do we find in the way of complete cell homologies, at the same time that marvelously close resemblances are brought to light. I admit fully the justice of the position taken by Conklin (see above, p. 465, first quotation), but I maintain that with the single exception of the apical rosette (and the cell $X_{1.2}$?) no organ of the annelid or mollusk has been traced back to a similar cell in enough cases to establish cell homologies or to justify Conklin's second statement (see above, p. 466, "We therefore," etc.).

This insistence upon a distinction between complete and incomplete cell homology may seem a quibble, but I believe the distinction is real, and that if we could prove complete cell homology, we would be led logically to a very different theory of development from what we must adopt if we regard homologies as incomplete or regional. If cleavage had the differential and determinate character urged by Wilson and Conklin, I do not see why all differential cleavages in gasteropods and annelids, or at least in two genera of annelids, should not show complete cell homologies. The number of divisions after differentiation might vary, depending on physiological needs of the organism, but *up to the stage of complete differentiation* I do not see why, on this theory, any incompleteness in the homology should appear. Conversely, if complete cell homologies do exist between the different groups, then the cleavage must have a differential and mosaic character. The evidence is, I believe, against both assumptions.

If cleavages are differential and have a phylogenetic significance, why should the mesoderm in Nereis not arise by the same number of divisions as in Podarke, since the two genera are pretty closely related? Why should Arenicola completely separate its mesoderm with the formation of 4d, while Aricia requires one more division, and Nereis three or four, to complete the separation between mesoderm and entoderm? Examples of this sort might be multiplied, showing, I believe, very grave difficulties in the way of cell homologies and determinate cleavage.

What explanation are we to give, then, for these remarkable resemblances? Are we to regard them as mechanically produced, and dependent upon conditions of pressure, temperature, etc.? Certainly not. I believe that these resemblances are due to homologies having perhaps a phylogenetic significance, but to homologies which are not bounded by definite cell areas. I believe that the prototroch, the paratroch, the supraoesophageal ganglia, the mesoderm, are to be regarded as homologous structures, and that the fact that they do not lie within corresponding cell walls in the different cases is an indication that we are here dealing with a regional as distinct from a cell homology.

Since the ancestral form made use of a certain cleavage pattern, secondarily moulding morphogenetic processes on cleavages which were primarily mechanical, we would naturally expect its descendants to follow in general the same cleavage design. Thus homologous organs, arising in corresponding portions of the embryo (as they naturally would in closely related forms) *might* arise in exactly the same cell, and cell homologies would appear; but these homologies are secondary and accidental, and found in no wide range of forms.

The fact that homologous organs have such a similar mode of origin in the cleavages of annelids and gasteropods, while not proving cell homology, is I think additional evidence in favor of the near relationship of the groups, as indicating not only an homology between corresponding portions of the adult, but between corresponding portions of the embryo as well.

The proper solution of the problem, it seems to me, lies along the line suggested by Whitman (No. 33, *c*), where he argues that we must regard the developing embryo as a complete organism possessed of a definite organization from the very beginning, and that the fact that this becomes split up into more or fewer cells does not affect this complete individuality. The embryo, like the adult, is an individual, not a collection of individuals, and it is governed by inherent force of its own, not by the mutual interaction of a number of forces. "Organization precedes cell formation and regulates it, not the reverse." "The structure which we see in a cell mosaic is something superadded to organization, not itself the foundation of organization." "The organization of the egg is carried forward to the adult as an unbroken physiological unity, or individuality, through all modifications and transformations" (No. 33, *c*). The difficulties I have pointed out in the way of cell homologies, as well as the facts of post generation in mutilated embryos, seem to me to strengthen this position.

I believe that, as originally stated by Wilson (No. 34, *d*), "The fundamental forms of cleavage are primarily due to mechanical conditions, and are only significant morphologically in so far as they have been secondarily remodeled by processes of precocious segregation"; and that the homologies which are found between different embryos are none the less homologies because they are not bounded by definite cell walls; nor does the fact that in some cases cell walls *do* bound homologous areas, have more than an accidental significance.

This position is not, I think, inconsistent with the explanation given before for the distinction between equal and unequal cleavage. I do not believe that the accidental accumulation of a certain amount of material in any particular cell necessarily implies that that material is, at the time of localization, differentiated. As a physiological rather than a morphological process, the egg has cleaved into a number of cells, and the organism, making use of these cleavage products, has stored in each variable amounts of material according to the needs of that particular region of the body. If this be true, there would follow a different explanation for the small size of some cells than the one given by Professor Wilson. He suggests that the small size of many cells in the cleavage stages indicates, like the degenerate organs of adults, degenerated structures which were once functional, but have in the phylogeny of the group become so functionless that they are now represented in the ontogeny merely by rudiments. (While this caution would possibly not apply to the small "mesentoblasts" of Nereis or Podarke, yet it should be remembered that mere size is in itself no indication of a degenerate condition. Cells which are very small when first formed may increase in size later and make up an appreciable portion of the embryo.)

If organs which are to appear early, or make up a large portion of the embryo, may be and are represented in the ontogeny by large cells, the converse of this proposition is correct, and the small size of many cells is due to the fact that the portion of the organism which is to arise from them is either small when formed, or appears late. (See above, p. 448.)

On this supposition portions of the embryo which are small are regarded as having a smaller amount of material set apart for them in the cleavage stages, and would thus be represented by smaller cells. Since these small cells are rarely the same in number (*cf.* the number of "mesentoderm cells" in the various cases), and their behavior is different in different forms (*cf.* the anomalous division of the cells corresponding to the prototroch in Chaetopterus, No. 22, Figs. 131 and 132), the rudimentary character of the cells must be regarded as individual variations, to be explained by the above assumption and not as an ancestral rudiment.

The most complete examples of rudimentary cells are not explained by either of the above assumptions. These are the small cells described by Conklin and Miss Langenbeck, and tentatively by myself in Podarke, as thrown off from the outside of the body, or absorbed into the segmentation cavity. These are hardly ancestral rudiments, and yet their fate is difficult to explain on the theory of precocious segregation of formative material. I can offer no satisfactory explanation of the phenomena.

OXFORD, OHIO, March 2, 1899.

NOTE. — Since this paper left my hands, March 2d, 1899, several important papers on cell lineage have appeared. See Appendix to Literature. Nothing in these papers has, however, led me to modify any of the views stated in the above.

VASSAR COLLEGE, January 5, 1901.

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DESCRIPTION OF PLATES.

In the following drawings no attempt has been made to represent the actual appearance of the cells, but only to indicate their size and position and the direction of the karyokinetic spindles. A peculiar feature of Podarke is the large size of the nuclei with their prominent chromosomes, the latter being especially prominent after staining with haematoxylin. These characters are not exaggerated in the drawings.

EXPLANATION OF PLATE XXXVI.

FIG. 1. First cleavage spindle, *pg*, polar globules.

FIG. 2. Two-cell stage from above.

FIG. 3. Four-cell stage from above.

FIG. 4. Eight-cell stage from the side.

FIG. 5. Eight-cell stage from above.

FIG. 6. Eight, forming sixteen cells. Formation of second quartette.

FIG. 7. Sixteen cells from the side.

FIG. 8. Sixteen, forming twenty-four cells. Formation of third quartette and intermediate cells.

FIG. 9. First division of primary trochoblasts.

FIG. 10. Twenty-eight to thirty-two cells. Division of second quartette.

FIG. 11. Thirty-two to forty cells from above. Formation of apical rosette.

FIG. 12. Forty cells forming fifty-six. Second division of trochoblasts and first division of intermediate cells.

EXPLANATION OF PLATE XXXVII.

FIG. 13. Thirty-two cells forming forty, from below. Formation of fourth quartette.

FIG. 14. Forty cells forming fifty-six, from the side. Second division of the trochoblasts, first division of the intermediate cells, and first division of third quartette.

FIG. 15. Fifty-six-cell stage from the side. Completion of the final division of the primary trochoblasts.

FIGS. 16–23. Successive stages in the history of the cross. *ap'* to *dp'*, primary trochoblasts. *ap''* to *dp''*, secondary trochoblasts. *ar* to *dr*, rosette cells.

FIG. 24. Second division of second quartette. Formation of $X_{1\text{-}2}$.

EXPLANATION OF PLATE XXXVIII.

FIG. 25. Completed division of second quartette in quadrant B.

FIG. 26. Completed division of second quartette in quadrant D, showing $X_{1\cdot 2}$. Bilateral division of 4d, $3c_2$, $3d_2$.

FIG. 27. Bilateral division of 4d, etc., from below.

FIG. 28. Third division of second quartette cell and first division of $3a_2$ and $3b_2$.

FIG. 29. Side view of preceding stage, showing A quadrant.

FIG. 30. Same as 29, showing D quadrant.

FIGS. 31 and 32. Division of X_3.

FIGS. 33 and 34. Formation of fifth group of micromeres.

FIG. 35. Division of $X_{1\cdot 2}$ and $3c_{2\cdot 1}$. Note the small superficial area of 4a, 4b, and 4c.

FIG. 36. First division of 4a, 4b, and 4c.

EXPLANATION OF PLATE XXXIX.

FIGS. 37 and 38. Formation of tertiary trochoblasts, ap'''_1, ap'''_2.

FIGS. 39 and 40. Divisions of X-cells.

FIG. 41. Stage of Fig. 38 from below. Note divisions of $3a_{2\cdot3}$, ap''' to d''', tertiary trochoblasts.

FIG. 42. Completion of division of X-cells, begun in Fig 40.

FIG. 43. Beginning of closure of the blastopore, and division of X. *Blp.*, blastopore.

FIG. 44. Division of $X_{2\cdot2\cdot1}$ and beginning of migration of "1" cells from the upper hemisphere.

FIG. 45. Division of X-cells and further migration of "1" cells.

FIG. 46. Further closure of the blastopore and division of $X_{1\cdot2\cdot1}$.

FIG. 47. Completed closure of the blastopore. *Proc.*, proctodaeum. *Stom.*, stomodaeum.

FIG. 48. A little later than 47. Complete concrescence of the X-cells on the ventral surface.

EXPLANATION OF PLATE XL.[1]

FIG. 49. Beginning of invagination of $3a_{2.2}$ (*l.m.m.*).

FIGS. 50 and 51. Division of $4d_1$ and $4d_2$ and of larval mesoblast. *l.m.m.*, median larval mesoblast; *l.m.r.*, right larval mesoblast; *l.m.l.*, left larval mesoblast.

FIG. 52. Second division of larval mesoblast.

FIG. 53. Final separation of definitive mesoblast and migration of larval mesoblast. Note migration of cells from upper hemisphere.

FIG. 54. Completion of divisions of Fig. 53.

FIG. 55. Next division of *l.m.m.* *l.m.r.* and *l.m.m.* have divided.

FIG. 56. Stage of Fig. 54 from the side.

FIG. 57. First division of definitive mesoblast. Note migration and large size of "l" cells.

FIG. 58. Completion of division of l_1 and division of $X_{3.2}$.

FIG. 59. Stage of forty hours from below. *M.*, mesoblast bands.

FIG. 60. Optical sagittal section of stage of forty hours. *en.*, entoderm; *ec.*, ectoderm; *ad.*, adoral zone; *ap.*, apical cilia; *pr.ap.*, preapical cilia; *pr.*, prototroch.

[1] In Figs. 49 and 50, $2b_{2.2.1}$. should read $2b_{2.2.1.2}$.

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FOUNDED BY JOHN D. ROCKEFELLER

THE CYTOGENY OF PODARKE OBSCURA (VERRILL)

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